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ALVARIÑO, ANGELES.
1985. Predation in the plankton realm; mainly with reference to fish larvae. Inv. Mar. CICIMAR 2 (NGm. Esp. 1):1-122. 8501

ALVARIÑO, ANGELES.
1985. Las surgencias en la region de California-Baja California relaciones con el zooplancton y poblaciones de *Engraulis mordax* (Pisces). Inv. Mar. CICIMAR 2(1):81-102 (in Spanish). 8502

ALVARIÑO, ANGELES.
1985. Distribucion batimetrica de especies del genero *Lensia* en aguas de California y Baja California (Diphyidae, Siphonophorae, Coelenterata). Inv. Mar. CICIMAR 2(1):59-80. 8503

ANKENBRANDT, LISA.
1985. Food habits of bait-caught skipjack tuna, *Katsuwonus pelamis*, from the southwestern Atlantic Ocean. Fish. Bull., U.S. 83(3):379-393. 8504

AU, DAVID W.K. AND WAYNE L. PERRYMAN.
1985. Dolphin habitats in the eastern tropical Pacific. Fish. Bull., U.S. 83(4):623-643. 8505

BAKUN, ANDREW.
1985. Comparative studies and the recruitment problem: Searching for generalizations. Calif. Coop. Oceanic Fish. Invest. Rep. 26:30-40. 8506

BALAZS, GEORGE H.
1985. History of sea turtles at Polihua Beach on northern Lanai. 'Elepaio 46(1):1-3. 8507

BALAZS, GEORGE H.
1985. Retention of flipper tags on hatchling sea turtles. Herp. Rev. 16(2):43-45. 8508

BALAZS, GEORGE H.
1985. Sea turtles and debris: Ingestion and entanglement. Mar. Turtle Newsl. 32:8-9. 8509

BALAZS, GEORGE H.
1985. Status and ecology of marine turtles at Johnston Atoll. Atoll Res. Bull. 285, 46 p. 8510

BALAZS, GEORGE H. AND WILLIAM G. GILMARTIN.
1985. A suggested modification of tagging pliers. Mar. Turtle Newsl. 34:2-3. 8511

BARLOW, JAY.
1985. Variability, trends, and biases in reproductive rates of spotted dolphins, *Stenella attenuata*. Fish. Bull., U.S. 83(4):657-669. 8512

TABLE OF CONTENTS (CONTINUED)

BARTOO, NORMAN AND TOSHIO SHIOHAMA.

1985. A production model analysis of the North Pacific albacore population including estimates of the sensitivity of results to measurement errors in input data. Bull. Far Seas Fish. Res. Lab. 22:109-117. 8513

BENVILLE, P. E., JR., J. A. WHIPPLE, AND M. B. ELDRIDGE.

1985. Acute toxicity of seven alicyclic hexanes to striped bass, *Morone saxatilis*, and bay shrimp, *Crangon franciscorum*, in seawater. Calif. Fish Game 71(3):132-140. 8514

BERKSON, J.M. AND D.P. DeMASTER.

1985. Use of pup counts in indexing population changes in pinnipeds. Can. J. Fish. Aquat. Sci. 42(5):873-879. 8515

BERNARD, HANNAH J., JOHN B. HEDGEPETH, AND STEPHEN B. REILLY.

1985. Stomach contents of albacore, skipjack, and bonito caught off southern California during summer 1983. Calif. Coop. Oceanic Fish. Rep. 26:175-182. 8516

BOEHLERT, GEORGE W.

1985. Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull., U.S. 83(2):103-117. 8517

BOEHLERT, GEORGE W. AND JOHN B. MORGAN.

1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasi*. Hydrobiologia 123:161-170. 8518

BOEHLERT, GEORGE W. AND MARY M. YOKLAVICH.

1985. Larval and juvenile growth of sablefish, *Anoplopoma fimbria*, as determined from otolith increments. Fish. Bull., U.S. 83(3):475-481. 8519

BOEHLERT, GEORGE W., DENA M. GADOMSKI AND BRUCE C. MUNDY.

1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull., U.S. 83(4):611-621. 8520

BRAINARD, RUSTY E. AND D. R. McLAIN.

1985. Subsurface temperature variability along the west coast of North and South America. Trop. Ocean-Atmos. Newsl., May issue:1-2. 8521

CASS, VIRGINIA L.

1985. Exploitation of California sea lions, *Zalophus californianus*, prior to 1972. Mar. Fish. Rev. 47(1):36-38. 8522

TABLE OF CONTENTS (CONTINUED)

CASTILLO, GONZALO, EDUARDO AGUILERA, GUILLERMO HERRERA, PATRICIO A. BERNAL, JOHN L. BUTLER, JAVIER CHONG, HUMBERTO GONZALEZ, CIRO OYARZUN, AND CARLOS VELOSO.
1985. Larval growth rates of the Pacific sardine *Sardinops sagax* off central Chile, determined by daily ring counts in otoliths. Biologia Pesquera 14:3-10. 8523

DeMASTER, DOUGLAS P.
1985. An analysis of a hypothetical population of walruses, pp. 77-80. *In:* F.H. Fay and G.A. Fedoseev (eds.), Soviet-American Cooperative Research on Marine Mammals, Vol. 1-Pinnipeds. NOAA Tech. Rep. NMFS-12. 8524

DeMASTER, D., D. MILLER, J.R. HENDERSON, AND J.M. COE.
1985. Conflicts between marine mammals and fisheries off the coast of California, pp. 111-118. *In:* J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne (eds.), Marine Mammals and Fisheries. George Allen Univ., Boston, MA. 8525

DUFFY, JOHN M. AND HANNAH J. BERNARD.
1985. Milkfish, *Chanos chanos* (Forsskal, 1775), taken in southern California adds new family (Chanidae) to the California marine fauna. Calif. Fish Game 71(2):122-125. 8526

FIEDLER, PAUL C., GARY B. SMITH, AND R. MICHAEL LAURS.
1985. Fisheries applications of satellite data in the eastern North Pacific. Mar. Fish. Rev. 46(3):1-13. 8527

GENIN, AMATZIA AND GEORGE W. BOEHLERT.
1985. Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. J. Mar. Res. 43:907- 924. 8528

GERRODETTE, TIM, DANIEL GOODMAN, AND JAY BARLOW.
1985. Confidence limits for population projections when vital rates vary randomly. Fish. Bull., U.S. 83(3):207-217. 8529

GOODING, REGINALD M.
1985. Predation on released spiny lobster, *Panulirus marginatus*, during tests in the Northwestern Hawaiian Islands. Mar. Fish. Rev. 47(1):27-35. 8530

GUILLEMOT, PATRICK J., RALPH J. LARSON, AND WILLIAM H. LENARZ.
1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). Fish. Bull., U.S. 83(3):299-311. 8531

TABLE OF CONTENTS (CONTINUED)

HEWITT, ROGER P.
1985. A protocol for designing a sea survey for anchovy biomass assessment, pp. 51-53. *In*: R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8532

HEWITT, ROGER P.
1985. Comparison between egg production method and larval census method for fish biomass assessment, pp. 95-99. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8533

HEWITT, ROGER P.
1985. Reaction of dolphins to a survey vessel: effects on census data. Fish. Bull., U.S. 83(2):187-193. 8534

HEWITT, ROGER P.
1985. The 1984 spawning biomass of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 26:17-25. 8535

HEWITT, ROGER P., GAIL H. THEILACKER, AND NANCY C.H. LO.
1985. Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. 26:1-10. 8536

HIGHTOWER, JOSEPH E. AND GARY D. GROSSMAN.
1985. Comparison of constant effort harvest policies for fish stocks with variable recruitment. Can. J. Fish. Aquat. Sci. 42(5):982-988. 8537

HOHN, ALETA A. AND P.S. HAMMOND.
1985. Early postnatal growth of the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 83(4):553-566. 8538

HOHN, ALETA A., SUSAN J. CHIVERS, AND JAY BARLOW.
1985. Reproductive maturity and seasonality of male spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific. Mar. Mamm. Sci. 1(4):273-293. 8539

HOLLAND, KIM, RICHARD BRILL, SCOTT FERGUSON, RANDOLPH CHANG, AND REUBEN YOST.
1985. A small vessel technique for tracking pelagic fish. Mar. Fish. Rev. 47(4):26-32. 8540

HOLLAND, KIM, RANDOLPH CHANG, AND SCOTT FERGUSON.
1985. Progress report on tuna tracking. South Pac. Comm. Fish. Newsl. 32:19-23 8541

TABLE OF CONTENTS (CONTINUED)

OLTS, DAVE.
1985. Recreational albacore, *Thunnus alalunga*, fishery by U.S. west coast commercial passenger fishing vessels. Mar. Fish. Rev. 47(3):48-53. 8542

UNTER, J. ROE.
1985. Preservation of northern anchovy in formaldehyde solution, pp. 63-64. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8543

UNTER, J. ROE AND BEVERLY J. MACEWICZ.
1985. Measurement of spawning frequency in multiple spawning fishes, pp. 79-94. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8544

UNTER, J. ROE AND BEVERLY J. MACEWICZ.
1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83(2):119-136. 8545

UNTER, JOHN AND RAGAN NICHOLL.
1985. Visual threshold for schooling in northern anchovy *Engraulis mordax*. Fish. Bull., U.S. 83(3):235-242. 8546

UNTER, J. ROE, NANCY C.H. LO, AND RODERICK J.H. LEONG.
1985. Batch fecundity in multiple spawning fishes, pp. 67-77. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8547

UPPERT, DANIEL D.
1985. Pacific coast groundfish management: Evolution and prospects, pp. 309-335. *In:* T. Frady (ed.), Proceedings of the Conference on Fisheries Management: Issues and Options. Univ. Alaska, Alaska Sea Grant Rep. 85-2, April 1985. 8548

UPPERT, DANIEL D., ROGER D. FIGHT, AND FRED H. EVEREST.
1985. Economic considerations, chapter 14, pp. 1-27. *In:* William Meehan (ed.), Influence of Forest and Rangeland Management on Anadromous Fish Habitat in Western North America. U.S. Dep. of Agriculture, Forest Service. Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-181, Portland, Oregon. 8549

ATO, SUSUMU AND STEPHEN C. SCHROETER.
1985. Biology of the red sea urchin, *Strongylocentrotus franciscanus*, and its fishery in California. Mar. Fish. Rev. 47(3):1-20. 8550

TABLE OF CONTENTS (CONTINUED)

KIRSCHVINK, J. L., M. M. WALKER, S-B CHANG, A. E. DIZON, AND K. A. PETERSON.
1985. Chains of single-domain magnetite particles in chinook salmon, Oncorhynchus tshawytscha. J. Comp. Physiol. A 157:375-381. 855

LASKER, REUBEN.
1985. What limits clupeoid production? Can. J. Fish. Aquat. Sci. 42 (Suppl. I):31-38. 855

LAURS, R.M.
1985. Application of satellite remote sensing to U.S. fisheries, pp. 755-763. *In:* Ocean Space Utilization '85. Proceedings of the International Symposium, Nihon Univ., Tokyo, Japan, June 1985. Springer-Verlag, Tokyo. 855

LAURS, R. MICHAEL AND JOHN T. BRUCKS.
1985. Living marine resources applications, pp. 419-452. *In:* Barry Saltzman (ed.), Satellite oceanic remote sensing. Adv. Geophy. 27, Acad. Press. 855

LAURS, R.M., R. NISHIMOTO, AND J.A. WETHERALL.
1985. Frequency of increment formation on Sagittae of North Pacific albacore *(Thunnus alalunga)*. Can. J. Fish. Aquat. Sci. 42(9): 1552-1555. 855

LO, NANCY C.H.
1985. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951-82. Fish. Bull., U.S. 83(2):137-150. 855

LO, NANCY C. H.
1985. A model for temperature-dependent northern anchovy egg development and an automated procedure for the assignment of age to staged eggs, pp. 43-50. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 855

MacCALL, ALEC D., RICHARD A. KLINGBEIL, AND RICHARD D. METHOT.
1985. Recent increased abundance and potential productivity of Pacific mackerel *(Scomber japonicus)*. Calif. Coop. Oceanic Fish. Invest. Rep. 26:119-129. 855

McLAIN, DOUGLAS R., RUSSELL E. BRAINARD, AND JERROLD G. NORTON.
1985. Nomalous warm events in eastern boundary current systems. Calif. Coop. Oceanic Fish. Invest. Rep. 26:51-64. 855

TABLE OF CONTENTS (CONTINUED)

MACKETT, DAVID J.
1985. Strategic planning for research and management of the albacore tuna fishery. Systems Res. 2(3):201-210. 8560

MOSER, H. GEOFFREY, ELAINE M. SANDKNOP, AND DAVID A. AMBROSE.
1985. Larvae and juveniles of aurora rockfish, *Sebastes aurora*, from off California and Baja California, pp. 55-64. *In:* A. W. Kendall, Jr. and J. B. Marliave (eds.), Descriptions of early life history stages of selected fishes. Third International Symposium on the Early Life History of Fishes and 8th Annual Larval Fish Conference, May 1984, University of British Columbia, Vancouver, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1359. 8561

MOSER, H. GEOFFREY AND ELBERT H. AHLSTROM.
1985. Staging anchovy eggs, pp. 37-41. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8562

MOSER, MIKE, JUDY A. SAKANARI, CAROL A. REILLY, AND JEANNETTE WHIPPLE.
1985. Prevalence, intensity, longevity, and persistence of *Anisakis* sp. larvae and *Lacistorhynchus tenuis* metacestodes in San Francisco striped bass. NOAA Tech. Rep. NMFS-29, 4 8563

NJOKU, E.G., T.P. BARNETT, R.M. LAURS, AND A.C. VASTANO.
1985. Advances in satellite sea surface temperature measurement and oceanographic applications. J. Geophys. Res. 90(C6):11,573-11,586. 8564

NORTON, J., D. McLAIN, R. BRAINARD, AND D. HUSBY.
1985. The 1982-83 El Niño event off Baja and Alta California and its ocean climate context, pp. 44-72. *In:* Warren S. Wooster and David L. Fluharty (eds.), El Niño north: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant Program, Univ. Washington, Seattle, WA 98195 USA. 8565

PARKER, KEITH.
1985. Biomass model for the egg production method, pp. 5-6. *In*: R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8566

PARRISH, R.H., D.L. MALLICOATE, AND K.F. MAIS.
1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83(4): 483-496. 8567

TABLE OF CONTENTS (CONTINUED)

PERRIN, WILLIAM F.
1985. The former dolphin fishery at St Helena. Rep. Int. Whal. Commn 35:423-428. 8568

PERRIN, WILLIAM F., MICHAEL D. SCOTT, G. JAY WALKER, AND VIRGINIA L. CASS.
1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis)* in the eastern Pacific. NOAA Tech. Rep. NMFS-28, 28 p. 8569

PERRY, ANJANETTE, GORDON B. BAUER, AND ANDREW E. DIZON.
1985. Magnetoreception and biomineralization of magnetite in amphibians and reptiles, pp. 439-453. *In:* J. L. Kirschvink, D. S. Jones, and B. J. MacFadden (eds.), Magnetite biomineralization and magnetoreception in organisms. Plenum Press, New York, NY. 8570

PERRY, S. F., C. DAXBOECK, B. EMMETT, P. W. HOCHACHKA, AND R. W. BRILL.
1985. Effects of exhausting exercise on acid-base regulation in skipjack tuna *(Katsuwonus pelamis)* blood. Physiol. Zool. 58(4):421-429. 8571

PERRY, S. F., C. DAXBOECK, B. EMMETT, P. W. HOCHACHKA, AND R. W. BRILL.
1985. Effects of temperature change on acid-base regulation in skipjack tuna *(Katsuwonus pelamis)* blood. Comp. Biochem. Physiol. 81A(1):49-53. 8572

PICQUELLE, SUSAN.
1985. Sampling requirements for the adult fish survey, pp. 55-57. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8573

PICQUELLE, SUSAN AND GARY STAUFFER.
1985. Parameter estimation for an egg production method of northern anchovy biomass assessment, pp. 7-15. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8574

PITMAN, ROBERT L.
1985. The marine birds of Alijos Rocks, Mexico. Western Birds 16:81-92. 8575

PITMAN, ROBERT L. AND MICHAEL R. GRAYBILL.
1985. Horned puffin sightings in the eastern Pacific. Western Birds 16:99-102. 8576

TABLE OF CONTENTS (CONTINUED)

POLOVINA, J.
1985. Variation in catch rates and species composition in handline catches of deepwater snappers and groupers in the Mariana Archipelago. Proc. Fifth Int. Coral Reef Congress, Tahiti, 5:515-520. 8577

POLOVINA, JEFFREY J.
1985. Artificial reef technology in Japan. ONRFE Sci. Bul. 10(4):15-20. 8578

POLOVINA, JEFFREY J. AND MARK D. OW.
1985. An approach to estimating an ecosystem box model. Fish. Bull., U.S. 83(3):457-460. 8579

POLOVINA, JEFFREY J., ROBERT B. MOFFITT, STEPHEN RALSTON, PAUL M. SHIOTA, AND HAPPY A. WILLIAMS.
1985. Fisheries resource assessment of the Mariana Archipelago, 1982-85. Mar. Fish. Rev. 47(4):19-25. 8580

RALSTON, STEPHEN.
1985. A novel approach to aging tropical fish. ICLARM Newsl. 8(1):14-15. 8581

SEAGARS, DANA J. AND JOHN R. HENDERSON.
1985. Cephalopod remains from the stomach of a short-finned pilot whale collected near Santa Catalina Island, California. J. Mamm. 66(4):777-779. 8582

SCOTT, MICHAEL D., WAYNE L. PERRYMAN, AND WILLIAM G. CLARK.
1985. The use of aerial photographs for estimating school sizes of cetaceans. Inter-Am. Trop. Tuna Comm., Bull. 18(5):383-419. 8583

SHOMURA, RICHARD S.
1985. Drift bottle makes long journey. Hawaii Fishing News 10(1):12 8584

SMITH, PAUL E.
1985. A case history of an anti-El Niño to El Niño transition on plankton and nekton distribution and abundances, pp. 121-142. *In:* Warren S. Wooster and David L. Fluharty (eds.), El Niño north: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant Program, Univ. Washington, Seattle, WA 98195 USA. 8585

SMITH, PAUL E. AND ROGER P. HEWITT
1985. Anchovy egg dispersal and mortality as inferred from close-interval observations. Calif. Coop. Oceanic Fish. Invest. Rep. 26:97-110. 8586

TABLE OF CONTENTS (CONTINUED)

SMITH, PAUL E. AND ROGER P. HEWITT.
1985. Sea survey design and analysis for an egg production method of anchovy biomass assessment, pp. 17-26. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8587

SMITH, PAUL E., WILLIAM FLERX, AND ROGER P. HEWITT.
1985. The CalCOFI vertical egg tow (CalVET) net, pp. 27-32. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8588

SQUIRE, JAMES L., JR.
1985. Relationship of sea surface temperature isotherm patterns off northwestern Mexico to the catch of striped marlin, *Tetrapturus audax*, off southern California. Mar. Fish. Rev. 47(3):43-47. 8589

STAUFFER, GARY AND SUSAN PICQUELLE.
1985. Procedures for sorting, staging, and ageing eggs, pp. 33-35. *In:* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36. 8590

SUMIDA, BARBARA Y., H. GEOFFREY MOSER, AND ELBERT H. AHLSTROM.
1985. Descriptions of larvae of California yellowtail, *Seriola lalandi*, and three other carangids from the eastern tropical Pacific: *Chloroscombrus orqueta*, *Caranx caballus*, and *Caranx sexfasciatus*. Calif. Coop. Oceanic Fish. Invest. Rep. 26:139-159. 8591

WAHLEN, BRUCE E. AND TIM D. SMITH.
1985. Observer effect on incidental dolphin mortality in the eastern tropical Pacific tuna fishery. Fish. Bull., U.S. 83(4):521-530. 8592

WALKER, MICHAEL M., JOSEPH L. KIRSCHVINK, AND ANDREW E. DIZON.
1985. Magnetoreception and biomineralization of magnetite fish, pp. 417-437. *In:* J. L. Kirschvink, D. S. Jones, and B. J. MacFadden (eds.), Magnetite biomineralization and magnetoreception in organisms. Plenum Press, New York, NY.9592 8593

WALKER, MICHAEL M., JOSEPH L. KIRSCHVINK, ANJANETTE PERRY, AND ANDREW E. DIZON.
1985. Detection, extraction, and characterization of biogenic magnetite, pp. 155-166. *In:* J. L. Kirschvink, D. S. Jones, and B. J. MacFadden (eds.), Magnetite biomineralization and magnetoreception in organisms. Plenum Press, New York, NY. 8594

TABLE OF CONTENTS (CONTINUED)

WHITTOW, G. CAUSEY AND GEORGE H. BALAZS.
1985. The thermal ecology of basking green turtles *(Chelonia mydas)*. Natl. Geographic Soc. Res. Rep. - 1977 Projects, pp. 789-796. 8595

ZUG, GEORGE R. AND GEORGE H. BALAZS.
1985. Skeletochronological age estimates for Hawaiian green turtles. Mar. Turtle Newsl. 33:9-10. 8596

The following publications are not included in the *Collected Reprints* 1985:

BALAZS, GEORGE H.
1985. Impact of ocean debris on marine turtles: Entanglement and ingestion, p. 387-429. *In:* R. S. Shomura and H. O. Yoshida (eds.), Proceedings of the Workshop on the Fate and Impact of Marine Debris, 26-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-54.

GERRODETTE, TIM.
1985. Toward a population dynamics of marine debris, pp. 508-518. *In:* R. S. Shomura and H. O. Yoshida (eds.), Proceedings of the Workshop on the Fate and Impact of Marine Debris, 26-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-54.

HENDERSON, JOHN R.
1985. A review of Hawaiian monk seal entanglements in marine debris, pp. 326-335. *In:* R. S. Shomura and H. O. Yoshida (eds.), Proceedings of the Workshop on the Fate and Impact of Marine Debris, 26-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-54.

LASKER, REUBEN. (Editor).
1985. An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS-36, 99 p.

LENARZ, WILLIAM H.
1985. Theoretical first approximations of densities of discarded webbing in the eastern North Pacific Ocean and Bering Sea, pp. 213- 217. *In:* R. S. Shomura and H. O. Yoshida (eds.), Proceedings of the Workshop on the Fate and Impact of Marine Debris, 26-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-54.

MORROW, ROBERT J. AND ELIZABETH. K. BUELNA.
1985. The Hawaiian monk seal and green turtle on Necker Island, 1983. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-55, 11 p.

TABLE OF CONTENTS (CONTINUED)

PARRISH, RICHARD H.
1985. Operational plan for NMFS albacore program. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-52, 31 p.

SHOMURA, RICHARD S. AND HOWARD O. YOSHIDA (EDITORS).
1985. Proceedings of the workshop on the fate and impact of marine debris, 26-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-54, 580 p.

SUND, PAUL N.
1985. Albacore fishing and windspeed. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-53, 18 p.

UCHIDA, RICHARD N.
1985. The types and estimated amounts of fish net deployed in the North Pacific, pp. 37-108. *In:* R. S. Shomura and H. O. Yoshida (eds.), Proceedings of the Workshop on the Fate and Impact of Marine Debris, 27-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-54.

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PREDATION IN THE PLANKTON REALM; MAINLY WITH REFERENCE TO FISH LARVAE

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RESUMEN

Se presentan y discuten los trabajos sobre depredación, en los organismos que sirven de alimento a los zooplanctontes carnívoros, incluyendo además información, que se encuentra dispersa en la literatura, sobre las dietas de los animales planctónicos carnívoros. Con esta revisión se establece la importancia que tiene el proceso de depredación en los mecanismos implicados en la supervivencia de larvas de peces.

Se recopilan los datos publicados y la información personal inédita, sobre la alimentación de las especies de los principales depredadores en el plancton; Medusas, Condróforos, Sifonóforos, Ctenóforos, Quetognatos, Copépodos, Eufáusidos, Anfípodos, Crustáceos, Decápodos, Poliquetos, Moluscos.

La información que existe sobre la dieta de los depredadores planctónicos indica, que estos animales tienen que ingerir alimento continuamente para subvenir a sus requisitos en proteinas, debido a su incapacidad de almacenar en el cuerpo sustancias de reserva. Esta particularidad se refleja en su comportamiento, alimentándose activa y continuamente. Estos voraces animales aparecen abundantes en los mares en todas las épocas del año, afectando el balance ecológico, y asimismo a las poblaciones de animales de importancia en las pesquerías.

La información publicada sobre especies planctónicas depredadoras y sus presas aparece recopilada en varias tablas.

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ABSTRACT

This discussion and presentation encompass published works on predation, food organisms of carnivorous plankton and pertinent dietary information included under different topics in the literature. The aim of this review is to elucidate predation and related subjects to better understand some of the mechanisms involved in the fish larvae survival.

Data are compiled on the feeding of main plankton predators; Medusae, Siphonophorae, Chondrophorae, Ctenophora, Chaetognatha, Copepoda, Euphausiidae, Amphipoda, Decapod Crustacea, Polychaeta, Cephalopoda, within the scope of the information published, together with personal unpublished data obtained along years of study.

The information on the dietary characteristics of most planktonic predators indicate that these carnivorous animals need to feed continuously to fulfill their requirements for protein intake, and their inability to store food reserves in their bodies, which is implied by their active feeding behavior. These voracious animals appear in large numbers in some years and areas, and this abundance affects the ecological balance of the environment, and subsequently the pupulations of animals of importance in the commercial fisheries.

Published information on predatory plankton species is compiled in tables.

INTRODUCTION

The marine fishes of commercial importance have an extremely high fecundity; mortality must, therefore, be correspondly high during certain life stages in order to give balance to the population. Joubin (1924) discussed this factor and stated, "mais tous ces petit poissons n'arrivent pas a leur état adult; leur destruction est intense et necessaire pour arriver à un equilibre entre la quantité de nourriture et le nombre de ceux qui la mangent".

Most mortality is believed to occur in the first few months of life (Gulland 1965, Lasker 1965, 1975, and May 1974); during the egg, larval, and juvenile stages. For example, in *Sardinops caerulea*, 99% mortality of the offspring occurs in a period from the egg to the pre-metamorphosed larval stage.

Many factors control the survival of eggs, larvae, and young fish, and it is widely accepted that abundance of eggs and strength of larval stages determine the size of the recruiting population (Ahlstrom, 1966). The magnitude of the recruiting fish stock is influenced by variables such as spawning (quality and quantity of eggs); the oceanic environment (mechanical effects related to disturbance of waves and currents); physical factors (temperature and light and currents which may transport the larvae into unfavourable environment); chemical factors (salinity, oxygen and pollutants); and biological factors such as food supply and predation. While the relations of most of these factors to abundance of fish generations have been independently analyzed, it would appear that combined analyses of the intrincate interaction of all the factors affecting the future of the fish generation are needed. Graham (1943) indicated, "wise administration of the Fisheries must work with the natural processes of the Sea".

An important part of the fishery investigations is the study of fluctuations in the relative strength of the different age groups (Hardy, 1956). "Identification of the mechanisms regarding recruitment will probably require the study of the entire larval and juvenil stages" (Hunter, 1979) in order to establish the difference between good and bad year classes (Baranenkova, 1961).

Research on the abundance of eggs and larvae began subsequent to Hensen's (1887) development of a method to estimate adult fish populations using calculations based on the number of eggs collected at sea. The abundance of the eggs spawned by several species of fish, together with measurements on the fecundity of females, enable investigators to estimate the total spawning stock. The number of eggs spawned will vary with the number of the adult fish on the grounds, but scarcity of one particular year class is not necessarily due to any decrease in the number of reproducing adults.

The survival of eggs, larvae, and juveniles, fluctuates throught the years; at times, a large adult population may give only a small number of recruits, and vice versa. Poulsen (1944) demonstrated a correlation between fluctuations in numbers of larvae and adult fish, that was based on larval generation; he believed that the frequency of a year class and its effects on the size stock (in this case cod) was already determined at the larval stage.

The analyses of factors involved in the life of fish indicate that the major causes of larval mortality are starvation - and predation, and that these interact with other environmental and biotic factors (Hunter 1976). Hunter (1979) states that in order to "identify mortality at sea, the incidence of starvation and predation must be estimated over the spawning range of the species and at all life stages, and these losses compared to estimated rates of mortality. "There is, however, disagreement as to which factor, starvation or predation is more influentia.

Until recently, more emphasis had been given to the lack of food as the main cause of larval mortality in many stocks of marine fish, because it was assumed that the rate of predatory mortality in the stock of fish larvae was mainly determined by the number of predators, with no consideration for their feeding capacity, and considering that the larvae were able to avoid the predators. Hempel (1965) further assumed that, "In many cases, years of high predator abundance are also years of rich food abundance for the fish larvae, and the food for the larvae is often also the main food for the planktonic predators".

The amount and quality of food available to the larvae does influence their survival, producing robust, healthy larvae; when food is scarce, larvae are weak, small, and more vulnerable to predation and sickness.

Losses by starvation are heavy, because larvae are small and require food of various qualities, sizes, and in specific quantities, at the various stages of the larval period (Lasker 1965). Murphy (1961) estimated the amount of food available for the calculated density of spawned larvae and found that food organisms for *Sardinops caerulea* appear to be "1 to 500 or 1 to 1500, or greater in 70 percent or 50% of the stations, respectively". He also calculated the distance each food item would be from the sardine larvae, and found it to be 5 cm to 3 cm or less.

Blaxter and Hempel (1963) have shown that larger sized eggs of *Clupea harengus* produce larger and healthier larvae which have a better chance of survival than those hatched from small eggs. However, feeding must be established before the yolk sac is absorbed, otherwise death of the larvae is unavoidable. In some cases, the survival capacity of larvae in laboratory experiments does not appear to be dependent on the size of the eggs, but rather on the availability of food (Ciechomski (1966) with larvae of Argentina anchovy). Apparently, both large size in normally constituted eggs, and suitable food are factors to be considered in the survival capacity of the larvae.

Although a number of publications deal with the planktonic food of fish larvae, the extent of mortality due to predation has not been thoroughly determined, even though this factor is widely accepted by marine biologists who consider that losses of larvae by predation may be high and related to the abundance and types of predators (Alvariño 1976b, 1977, 1979 and 1980b). While starvation cannot be clearly evidenced in the field, predation is a real phenomenon, observed by planktologists when analyzing the plankton material, because fish larvae, under various degrees of digestion, can be seen inside the predators' digestive tract.

In addition to these biotic factors, the mortality of fish larvae may also be affected by abiotic factors such as wave action and light intensity (Hempel and Weikert 1972, Pommeranz 1974). Wave action has for a long time been considered a cause of severe mortality of pelagic fish eggs (Rollefsen 1930, 1932; Devold 1935; Zaitsev 1968, and Pommeranz 1974). Ultraviolet light may be dangerous to pelagic eggs and larvae when they are close to the surface waters (Marinaro and Bernard 1966; Hunter, Taylor, and Moser 1979), and light also appears to be more harmful to demersal eggs which usually develop at low light intensities. In addition, "the vertical position of larvae in the sea in relation to their food, predators and time of day needs to be considered" (Hunter 1979), as does water temperature.

Temperature during incubation and during yolk sac stages affects duration of development and eventual survival of the larval stage (the most vulnerable period in the life cycle of fish), and also the metabolic activity of the fish.

All these factors, both biotic and abiotic, interact in different ways and degrees, on fish larvae, their prey species, and their predators. Some of these interactions are discussed in the following examples.

In the California region, the most outstanding ocean feature is the California Current System, which affects the temperature of the ocean in this region and the quality and abundance of its faunistic complex. From 1944 to 1956 temperatures in the oceanic region off California were lower than usual, and from 1957 to 1960 temperatures were higher than usual. Tempera tures from 1960 to 1964 were lower than those in the early fifties. From 1965 to present temperatures in this region could be considered high, on the average (with some yearly fluctuations) but not as high as for the late 1950's. Historical records (Murphy 1961) indicate that "warm years tend to be associated with good year classes and cold years with poor ones" for sardine. He examined the possibility that cold temperatures may increase larval mortality due to predators or/and that cold temperatures are associated with other factors affecting the sardine population. He also suggested that low temperatures might prolong the larval phase, lengthening the vulnerability of the larvae to predation.

Data I obtained during my studies of the plankton off California indicated that the abundance of predators (mainly chaetognaths) is greater during cold years than during warm years. In addition, they are of larger size, and their populations cover a larger area of the California Current Region. Low temperatures prolong the larval stage of the fish, increasing their vulnerability to the eventualities of the oceanic environment, including predation. During cold periods, the predatory organisms present are more abundant, of larger size, and are at their peak of predatory capacity. These predators not only feed on fish larvae, but also compete for food with the fish larvae and plankton consuming fish.

ZOOPLANKTON PREDATION

Fish larvae mortality by predation has been discussed by Lebour 1922, 1923 and 1925; Bigelow 1926; Murphy 1961; Fraser 1969; Hempel 1965; Dekhnick et al 1970, etc., and the analysis of the literature related to mortality of fish larvae indicates that predation may be responsible for a high toll. Indeed, Johannes (1978) in discussing strategies of reproduction in fishes, indicates that "predation appears to be more important than availability of food in influencing where, when and how many (Tropical marine) fishes spawn and where their eggs and larvae are distributed".

The younger growth stages of fish consitute part of the plankton realm. Although the study of changes in the plankton holds "important keys to a better understanding of success of failure in the fisheries" (Hardy 1956), little has been published on the feeding activity of the main predatory organisms of the plankton realm. What is known on the subject is scattered through the literature, in few lines included in works not dealing specifically with predation.

Murphy (1961) considers that "fish larvae will be subject to roughly the same rate of predation, as have other organisms in the plankton possesing the same general dimensions and behavioral characteristics". Predation therefore, can become an important factor in the study of fish populations, particularly of food. Murphy (1961) believes that "the intense predation typical of the plankton community is responsible for the rapid decline in numbers of sardine larvae, and variations in this rate of predation are primarily responsible for variations in the rate of survival. Medusae, Chondrophora, Siphonophorae, Ctenophora, Chaetognatha, pelagic Polychaeta, and other carnivorous zooplankters not only impose a heavy toll on the delicate fry of many fish species, but also compete with them for the same food. These voracious animals are present in great numbers in some years and areas, affecting the ecological balance of the micro-environment of the oceans.

The diagram (Fig. 1 in Alvariño 1976b) of plankton volumes and average number of Chaetognatha for 1954 and 1958 off California shows that large volumes of zooplankton correspond to low number of chaetognaths and vice versa. In addition, high volumes of zooplankton only in few cases coincide with good generations of anchovy larvae. (Note: plankton volume is a magnitude which does not provide proper biological information relative to the micro-environment. Different types of organisms are integrated in that volume, which are not accounted for and could be critical to the study. Volume of samples are numbers with no major biological significance, and should not be used to draw biological conclusions. The term "plankton" encompasses all the zoological invertebrate groups at any stage of development in the ocean, including the vertebrates, fish eggs and larvae. It is therefore necessary to know not only the amount, volume, or number for each of the plankton groups in the plankton sample, but also the abundance of each of the species integrated into the total volume of plankton).

Strasburg (1960) compared data on tuna larvae (*Katsuwonus pelamys* and *Thunnus albacares* combined) and invertebrate plankton volumes; and he found that large catches of tuna larvae coincided with small or moderate volumes of plankton, while poorest and richest catches of plankton contained few larvae. Large number of zooplankters coinciding with low numbers of fish larvae could indicate that predators were abundant in the plankton, and have been devouring tuna larvae. Small plankton volumes and high numbers of tuna larvae imply that plankton present served as food for the tuna larvae and that few or no predatory species were present. The consideration on this indicates that, it is not advisable to compare facies, such as fish larvae and plankton, as Strasburg has done, when one of the factors, plankton, includes many unidentified species. There is need to explain the abundance of each of the species included in the plankton volume being discussed.

Analysis of zooplankton and fish larvae collected at the low part of the Newport River Estuary, North Carolina (Thayer et al 1974), indicates both an increase in the zooplankton abundance prior to the seasonal immigration of larval fish into the estuary and a general decrease in zooplankton during the period of larval abundance. Copepods were dominant in most collections (comprising up to 81% of the zooplankton) and the rest included barnacle larvae, ostracods, cladocerans, crustacea larvae, and chaetognaths. These data demonstrate the inverse relation in abundance between fish larvae and their food; a decrease in one indicates an increase in the other. This inverse relation between number of larval fish and the volume of plankton was also noted by Ali Khan and Hempel (1974) in the collections from the Gulf of Aden. Studies by Harding and Talbot (1973) in the southern part of the North Sea showed that, in general, the abundance of eggs and larvae of *Pleuronectes platessa* (plaice) was inversely related to abundance of predators.

The copepods *Acartia*, *Centropages*, *Euterpina*, and *Temora* appeared to be the major food items of larval fish in the Newport River estuary, declining from a mean of 81% of the biomass in March to a mean of 48% during June-July for the years of survey, 1970-1972. Thayer et al (1974) thus stated, "Maximum densities of fish larvae coincided with the period of zooplankton decline". However, the diagrams included in the work do not show a sharp relation of those parameters for 1970 and 1971, and the situation of the plankton during part of 1972 is unknown as plankton data for this year only covered January to April. In 1970 the zooplankton peaked precisely in March-April, but in 1971 the peak occurred in May, after rising from a low value in February. Thayer et al (1974) found some discrepancies in their calculations due to the fact they only considered two factors, fish larvae and plankton as food, neglecting type of plankton, abundance of food items, and abundance and identification of plankton predators on fish larvae.

Studies on the distribution and survival of *Clupea pallasi* Vallenciennes (herring) larvae in the British Columbia waters (Stevenson 1962) indicate that predation, lack of food, and temperature were not considered mortality factors at inshore waters, the loss of larvae was due to seaward transport of the larvae by currents. However Stevenson did observe predation by Ctenophora, Medusae and Chaetognatha on herring larvae during the period of study, 1947 to 1951. Although the species of predators and their abundance were not determined; Stevenson considered only percentage of predators as evidenced in the actual sampling, with no information on the relation between number of individuals per predatory species and their predatory capacity, and co-occurrences with fish larvae. Lucas and Henderson (1936) discovered that good catches of herring were not usually taken where jellyfish abounded. Poulsen (1944) reviewed the results of a series of plankton observations and the occurrence of young cod in the Danish region for the period of 1932 to 1933, and found a correlation between the number of young cod in ring trawl catches in April and May and the kind of plankton in the same region, and Hunter (1984) analysed relation of cod larvae and predation.

Study of the vertical distribution of the larval and post-larval stages of fishes of commercial importance (Russel 1925) in the British Isles region, were related to their occurrence with other organisms, including both food and predators. The numerical abundance of the Chaetognatha *Sagitta elegans* and *S. setosa* in the Atlantic region off the English channel (Russel 1933) together with abundance of Copepoda, other Crustacea, Medusae, Siphonophorae, and Ctenophora in 1930 collections were compared with young fish data for the same collections (Russel 1935a). The analysis of these data indicates that abundance of young fish was coincident with rich food plankton, and low concentration of young fish coincided with great abundance of Medusae, Siphonophorae and Ctenophora. It was observed in the same set of data high concentration of *S. elegans* occurred in waters rich in *Calanus finmarchicus*, *Metridia lucens*, *Candacia armata*, *Anomalocera patersoni*, and zoeas; and low concentration of *S. elegans* and/or high abundance of *S. setosa* was coincident with high concentration of species of Medusae, Siphonophorae and Ctenophora.

Studies on changes in abundance of fish larvae off Plymouth, England, were related (Russell 1935b) to variations in environmental conditions, mainly temperature and availability of adequate food supply for the larvae (important factor in the success of the year class), and abundance of predatory planktonic organisms. The results showed absence of the normal peak of abundance of fish larvae from spring spawning fish, probably due to concurrence of large number of Ctenophora.

The bulk of the spawning population of fish from the Atlantic waters (Russell 1936) spread over the English Channel region and the plankton rich Atlantic water (identified by *S. elegans*) permitted high survival of young fish, while Channel waters characterized by *S. setosa* concurred with scarcity of young fish. *S. elegans* waters contain abundant food supply, while *S. setosa* waters included abundance of planktonic predators, which contributed to the depletion of the food supply. Russell in several of his papers, related the success of young fish population to the co-occurrence of rich waters, and their failure to the presence of poor waters and abundance of predatory animals.

Observations along series of years at Plymouth (Russell 1952) indicated that waters rich in phosphates increased the abundance of plankton and hence the survival of young fish populations. That is, abundant rich plankton will substain a high survival value for fish larvae. However, rich water could not necessarily lead always to a good survival rate, as happened in 1939 off Plymouth, when fertile waters were present and the peak of young fish was absent, but Ctenophores abundant.

Zooplankton from 40 locations in the Great Barrier Reef Lagoon, Australia, 3 miles east of Low Isles (Russell 1934) included numbers per station of protozoa, Medusae, Siphonophorae, Chaetognatha, Polychaeta, Ostracoda, Copepoda, Mysidacea, Amphipoda, Euphausiidae, Appendicularia, Thaliacea, Pteropoda, Heteropoda, fish larvae and eggs and larvae of Echinodermata, Crustacea, and Mollusca. Analyses of these data indicate that high concentration of Chaetognatha, Medusae and Siphonophorae coincided with low concentration of fish larvae, although apparently Copepoda appeared more or less consistently abundant in all stations. The percentage of predators (Medusae, Siphonophorae, Chaetognatha, Stomatopoda larvae, fish larvae) of the total zooplankton at the Great Barrier Region was 3.1% compared to 5.0% in The North Sea (Russell 1934).

Observations and experiments evidence that Chaetognatha, Siphonophorae, Medusae, Chondrophorae, Ctenophora and in less degree other zooplankters, feed voraciously on fish larvae (Lebour 1922, 1923, 1925), which are often found in the stomachs of individuals belonging to the mentioned planktonic groups. Bigelow (1926) explains that the organisms to be studied in relation to the survival of fish larvae are: "Medusae, Ctenophores, Sagitta and Crustacea that prey upon them, and so many species are plentiful in the Gulf of these groups are known to prey on fish larvae that they are almost certainly the most effective check on the survival of the countless myriads of young fish that are yearly produced in the Gulf. There is good reason, then to believe that the fluctuations known to occur from year to year in the stocks of herring, mackerel, haddock etc., which are reared in the Gulf, depend more on the abundance of the rapacious members of the planktonic community (and especially on the abundance of *Sagitta*, Medusae, *Pleurobrachia*, and *Euthemisto*) than on any other factor. If plankton studies need any defense from the standpoint of fisheries we need look no further".

Anchovy abundance off California coincided with abundance of Copepoda and Euphausiidae, and scarcity or absence of anchovy larvae with abundance of Chaetognatha (mainly those of high predatory potential and large size), Siphonophorae, Medusae (Alvariño 1980b), and scarcity of Copepoda and Euphausiidae.

Predation studies on fish larvae imply the species competition in the plankton, and the proper identification of the organisms which are potential food for the larvae; their quantities, food value, and predatory capacity.

Lebour (1922, 1923, 1925), Bigelow (1926), Fraser (1969) observations and analyses of food in species of Chaetognatha, Medusae, Chondrophorae, Ctenophora, Polychaeta, and other zooplankters, indicate that these transparent and delicate creatures are very voracious and are in a continuous feeding process.

Scarce attention has been dedicated to the predatory effect of a small predator *Noctiluca*, present in high aggregations in the oceans. The occurrence of dense patches of this dinoflagellate occurred at the spawning areas of Clupeidae and Engraulidae. It feeds on diatoms, dinoflagellates, protozoans, Cladocera, Nauplii and copepod eggs and juveniles, *Oikopleura* (Enomoto 1956), and the eggs of *Sardinia melanosticta* and *Engraulis japonica* (Enomoto 1956, Hattori 1962). *Noctiluca miliaris* (Syn, with *N. scintillans*) was observed feeding on *Acartia clausi* (Seguchi and Kato 1976) and *A. tonsa* eggs (Kimor 1979). Published information and observations of enormous aggregations of *Noctiluca* at the bays of Northwest Spain feeding on *Sardina pilchardus* eggs and copepods, and other zooplankters (personal observations) indicate a direct effect on the survival of fish, and indirectly as competitors for food with the fish larvae, by using the food available.

Newly hatched and young fish have little chance against all these enemies, as they are an important food supply for the above mentioned zooplankters. Compiled information on the general diet of most of the important planktonic groups indicate that these carnivorous zooplankters need to feed continuously to fulfill their need for high protein intake and inability to store food reserves in their bodies.

PREDATION BY COELENTERATES

Coelenterates are active predatory carnivores, considered by Bigelow (1926) to be the most destructive of the small and delicate animals in the oceans. Duvault (1965) and Alvariño (1976a,b) indicated that they feed exclusively on living animals, primarily small invertebrates and fish larvae.

The basic feeding behavior of Colenterates (Medusae, Chondrophorae, Siphonophorae) in the plankton, and in some extent also in the Ctenophora, rely on some poisonous mechanisms. They have developed a unique system which produces venom to inject into the body of the prey or any item coming close to or in contact with them. The nematocyst, cnidocyst, or nettlecells are filled with a toxin which is discharged by coiled tubes into the victim. In small animals the poison produces a paralyzing effect which becomes lethal. The toxin may even kill humans and other large animals.

MEDUSAE

Medusae are beautiful, delicate animals, both in form and color. Mayer (1917) explained that, "No class in the animal kingdom exhibits a more surprising variety of forms than do the jellyfish and their close allies the Siphonophorae". Medusae present multitude of shades of colors and hues, ranging from dark purple to red, to brown, with many crystal clear specimens; the tonality or color is not specific in many cases. The coloration in some medusae may be a protection against ultraviolet rays light (Ries and Ries 1924).

Medusae are of interest to study in relation to faunistics, ecology, indicators of ocean currents, predation, and in modern pharmacological studies related to medical research. Medusae (Hydro-and Scyphomedusae) are exclusively carnivores, and their growth rate and size reached at maturity is related with the quality and quantity of food available.

The Medusae detect and localize the potential prey with the aid of the statocyst, sensing the vibrations produced by moving water. They prey on actively swimming animals, such as Copepoda, other Crustacea and their larvae, and the larvae of fish and other groups. The victim is paralyzed by the tentacles of the Medusae with the poison produced in the stinging cells; the prey is later ingested in the Medusa's stomach. Medusae may inject 3 cc poison by a single discharge.

Medusae are considered important in the destruction of eggs and larvae of cod (Mayer 1917) and other fish. They may be the primary enemies of young fish (Joubin 1924). However, while fish may become entangled, trapped, and poison within the tentacles, the larvae and young of some species of fish are known to aggregate under the umbrella of large Scyphomedusae, living together in an apparent biological association. The offspring of some fish may be protected under the canopy of the Medusae's umbrella from the attacks of other animals, while themselves avoiding the proximity of the Medusae. The smooth vibrations produced during swimming by various fish larvae and young fish may not excite the nematocysts of the medusae and no releasing reaction occurs. In underwater observations on association of Scyphomedusae (110 mm diameter) *Acromitus flagellatus* Stiasny and young fish 10.6 to 30.0 mm long *Seleroides leptolepis* (Carangidae), Jones (1960) noted that "the fish kept themselves close to the medusa but not in actual contact with it. Their movements were so well synchronized that it would appear that the fish, which were never seen to turn round or make any special attempt to check the position of the jellyfish, could anticipate the direction in which and the distance to which the later would move". Similar observations were made for the Medusae *Mastigias papua* L. Agassiz and the fish *Caranx kalla;* in both cases, the fish appear swimming slightly ahead of the medusae.

It has been implied that Medusae's poison does not affect some species of fish, which become immune to the medusae's -

toxin; but there is not enough available evidence to totally prove this matter. Some of the fish and larvae do in fact get poisoned and devoured by the medusae, but other remain alive, sheltered, and protected up to the time close to adulthood. This biological association could be considered a case of mutualism, which supplies a source of fresh, live food for the medusae, and protection for some of the young fish surviving through the most critical period of their life history.

I have observed large number of Scyphomedusae off Plymouth (England), Vigo (Spain), Callao (Peru), San Diego (California, United States), appearing in areas concurrently with concentrations of Clupeidae, Engraulidae, Trachuridae, Merluccius, Gadidae, etc. The young of some species of fish tend to swim towards the shelter of any floating object at sea, and large Scyphomedusae offer an ideal canopy shelter. Young fish may also be lured by the swift gliding tentacles of the Medusae, and they swim towards them. Some become trapped and are devoured, while other continue to enjoy shelter and protection until they have grown to the stage where they can independently move out as recruits of the adult population.

These associations have been widely observed. Osterbol (1885) noted young mackerel and young cod sheltered under the Scyphomedusae umbrella, and observed that occasionally the medusae "snatch a fish, which therefore has to pay with its life for the protection that still other comrades are enjoying". - Mayer (1898) found two species (a Clupeididae and a Butterfish) accompanying the Scyphomedusae *Chrysaora* (*Dactylometra*) *quinquecirrha*. Damas (1909a,b) noted that *Cyanea lamarcki* in the North Sea appeared often associated with young pollak (*Gadus pollachius*), poor cod (*G. minutus*) and pouting (*G. luscus*). Underwater observations have also showed young *G. merlangus* (whiting) swimming and moving around and above *C. lamarcki's* umbrella (Rees 1966). In fact, the vertical distribution of *C. lamarcki* (as *C. capillata*) appears to be correlated with the vertical distribution of whiting. In the English Channel off Plymouth, whiting 12-22 mm long appear to associate with medusae of all sizes, while those of more than 25 mm were associated with medusae 100 mm or more in diameter (Russell 1928). - Young *Trachurus trachurus* 11-15 mm in length also appeared associated with *C. lamarcki* (as *C. capillata*) in the Plymouth area (Russell 1930 a,b).

Nagabushanam (1959) mentioned three young *Gadus morhua* gathered under the Scyphomedusae, one of which had ingested

Hyperia (Amphipoda considered associated or ectoparasite of Medusae) and to *G. luscus* larvae 33-45 mm long. *Rhizostoma* sp. swimming against the tide together with an aggregation of *T. trachurus* were observed by Browne (1900), Phillips (1971) found the medusae *Stomolophus meleagris* associated with various young fish (*Trachurus*, *Peprilus*, *Poronotis* and *Chloroscombrus*). *Poronotis burti* were found in association with *Cyanea capillata* and *Stomolophus meleagris*. *Chloroscombrus chrysurus*, *Peprilus paru*, *Trachurus trachurus*, *Monocanthis hispidus*, appeared associated with *Chrysaora*, and *Stomolophus meleagris* with *Cyanea capillata versicolor*. *Cyanea capillata* is often found sheltering young whiting (*Gadus merlangus*), the mackerel (*T. trachurus*), young cod (*Gadus callarias* or *G. morhua*), and haddock (*G. aeglefinus*).

Beebe and Tee-Van (1928) described the high number of young fish (*Chloroscombrus* (*scomber*) *chrysurus*) or bumber, 12.5 to 47 mm long and 22 mm *Peprilus paru* (harvest fish) captured under the medusae *Chiropsalmus*, *Tamoya haplonema*, and *Cyanea* of about 100 cm diameter in the Port-au-Prince Bay. Lowles (1877) and Romanes (1877a,b) found young fish occasionally associated with *Aurelia aurita*, swarms of one to two-year old *Gadus merlangus* appeared under the Scyphomedusae, and large numbers of *A. aurita* were concurrent with dense aggregations of this -Gadoid.

Mansueti (1963) reported *Peprilus alepidotus* (harvest fish) and *Poronotus triacanthus* (butterfish) in association with *Chrysaora quinquecirrha* from July to October in Chesapeake Bay. Small pieces of the medusae tentacles and oral lappets were obtained from the stomach content of *Peprilus*, and nematocysts could be observed on *P. alepidotus*. These fish, when placed in an aquarium, developed infectious spots on the body, swam in an erratic manner, displayed loss of equilibrium, and finally died. All signs of fish being poisoned. Other *P. alepidotus* not associated with scyphomedusae did not show any of those symptoms, and remained alive por a long period of time in the aquarium. My observations of *Gadidae* *Merluccius* and *Trachurus* larvae with *Cyanea* and *Chrysaora* indicated that the fish were not very active and a high proportion of them were under the effect of the toxins from the Medusae. Experiments carried by Dahl (1961) provide the conclusion that "young fish initially use medusae for shelter, thus reflecting simple thigmotaxis". The fish may later be stung by the host and, "if the fish touches places with no stinging cells, there is an accidental association".

These associations may be influential in the brood dissemi nation of the offspring of fish (Damas 1909 a,b). In the material I have studied from the English Channel, *Trachurus trachurus* and *Gadus merlangus* larvae appeared associated with *Cyanea lamrcki* a medusae inhabiting mainly the coastal regions. These medusae may also be carried far offshore and transported to other latitudes by currents, carrying with them the associated fish fry.

Considering the huge quantities of Medusae and their size range, from a few millimeters to about 1000 mm or more in diameter, and their world wide oceanic distribution and particulary great concentrations in the fishing regions, these animals may play an important role in the recruitment of fish and in relation to the commercial fisheries. Mayer (1910) in his Medusae of the World listed 737 species of Medusae, primarily marine, and Kramp (1961) mentions more than 800. The published literature shows direct observation of 65 of these species of Medusae, eating fish larvae and young fish, and/or planktonic animals. These observations are compiled in Table 1, and indicate that fish larvae are the preferred food items. Lebour (1922) explained that the Medusae she observed would feed exclusively on fish larvae when those were available in any quantity.

In 1768 Slabber observed a medusae feeding on fish and in 1778 published this observation of the medusae he named *Medusa cymbaloides* (probably *Phialidium hemisphaericum*) devouring a young fish. Slabber*s brief comments appear in Gudger (1937): "As soon as I had caught it, I placed it under the microscope and found that it had caught a very small fish for its prey, which could still be seen outside of the body...(the fish) was only lively when I looked at it, and one could see plainly that it was being drawn in. Thus drawn in was completed in two hours time, and then the whole creature..." Slabber had already realized that the millions of medusae in the North Sea might consume a great amount of fish, which would effect the number of fish later available for commercial fishing. K. Nair (1947) analyzed the Medusae and fisheries of the Travancore coast, India, and found that large concentrations of Medusae during certain seasons affected the fisheries destroying fish eggs and larvae as well as other organisms which constitute the food of small fish. In addition, studies of the zooplankton on the Bombay region (Bal and Pradhan 1952) show that a minimum number of fish larvae and post larval stages coincide with high numbers of hydromedusae.

Phialidium hemisphaericum (probably the first medusae observed feeding on fish larvae by Slabber in 1768, devour almost exclusively young fish (Lebour 1922), which constitute its whole diet when available in quantity. Bigelow (1926) discussed the great abundance of *P. hemisphaericum* which, together with *Aurelia aurita*, he considered the two most abundant Medusae of the coastal and open waters of the Gulf of Maine. They are proven eaters of fish, euphausiids, copepods, appendicularian and various larvae, and "must take heavy toll of the little fish that cross their paths". Gudger (1937) reported that "at the high of the herring spawning season in the vicinity of the Bay of Fundy, it was found that *Phialidium* formed an important enemy of the fry"; of the 356 herring larvae collected in one station, 16 were in the stomach of *Phialidium* and other 53 were partially digested.

Orton (1922) described in detail the feeding process and characteristics of Medusae. The analysis of the food pouches in *Aurelia* showed that the Medusae devour various kinds of planktonic organisms as well as some of the young fish taking shelter under its umbrella. A typical meal for *Aurelia aurita* from early ephyra into large adult state includes 16 small fish (*Cottus or Blennius*), which were eaten (Lebour 1922) in less than 30 minutes, and if fish were not available, amphipods, zoeas, other crustaceans, and medusae were eaten. Gudger (1937) reported that Fish in 1924 indicated that *A. aurita* fed on winter flounder larvae in the New England region and that in Waquoit Bay "where both animals breed in abundance, *Aurelia aurita* proved of very vital importance in depleting the flounder stock".

Russell (1970) indicates that "in view of their size and abundance the Scyphomedusae must play a large part in the economy of the sea as predators and competitors of fish". Hela (1951) commented on the inverse relation found on the abundance of sprat and herring larvae with the abundance of *Aurelia aurita* off Finland, and Lebour (1922) observed a similar relation for the British Isles, where huge concentrations of *A. aurita* coincided with nil catches of fish.

Yasuda (1970) calculated the biomass patches of the medusae *Aurelia aurita* in Urazolo Bay, Japan, in the range of 1.4 to 9.2 tons. These medusae are mainly abundant in the upper 10 m; their distribution is thus closely related with the epipelagic fish larvae and the abundance of the medusae will reduce drastically that of the larvae. Studies on the ecology of zooplankton (Neale and Bayly 1974) in the Patterson, Yabarra, Maribyrnong, and Werribee River estuaries in Victoria, Australia, on fish eggs and larvae, copepods, crustacea larvae, mollusks, echinoderms, inmature *Aurelia* sp. medusae and *Australomedusa baylii* Russell in the Werribee area coincided, in one case, with no fish eggs or larvae.

Cyanea capillata is another medusae which effects commercial fisheries. It reaches a large size, more than 1 m in diameter, and has numerous tentacles which spread through the waters while moves by jet propulsion produced by rhythmic pulsations of the umbrella. It engulfs enormous quantities of zooplankters as it glides through the water. Russel (1970) stated that, "a Northeast coast fisherman told me that he had heard that *Cyanea* preyed on planktonic lobster and that a poor lobster fishery might result four years after a year of great abundance of these hellyfish. This seems to me quite possible".

Russell (1931), and Lucas and Henderson (1936) have suggested that the abundance of *Gadus merlangus* may be correlated with the abundance of large *Cyanea* in the North Sea. Lucas and Henderson (1936) examined the reports of fishermen on the incidence of several species of Medusae with catches of *Clupea harengus* and concluded that "large catches of herring were related to low abundance of medusae, including *Cyanea capillata*". They also indicated instances of medusae occurring in certain areas of herring fishery, coincident with nil or extremely poor catches of herring. In all cases, the herring were taken outside the zone where these medusae were present. The information compiled by Lucas and Henderson (1936) indicates a definite inverse relation between low quantities of herring and abundance of medusae.

To further investigate this relation, Russell (1938) added the average monthly catches of Medusae for 1920-1937, and the total young fish (excluding Clupeidae). The numerical data show that values for 1931, 1932, 1934, and 1935 included low numbers of medusae coinciding with high numbers of young fish. Similar results, although in a different order of magnitude for the fish, were found for 1936 and 1937. However, the number of Clupeidae larvae was not included in the listings, so it is not possible to obtain a clear picture of the situation; the number of Clupeidae larvae could be an important factor in the final determination of the relation of fish larvae and Medusae. It is possible that in 1930, year of highest amount of Medusae and no of lowest amount of fish larvae (excluding Clupeidae), the medusae could be feeding on herring or sardine, and thus the abundance of medusae would not affect the abundance of larvae of other species of fish.

Liriope tetraphylla is the most abundant medusae in the warm and temperate oceanic regions. A voracious predator, it captures prey up to three times its own size (McCrady; 853; Fraser 1969). Candeias (1931) stated that in June 1926 huge quantities of *L. tetraphylla* coincided at Olhae, off Algarves coast, Portugal, with total lack of *Sardina pilchardus*, in a region where this Clupeidae is abundant. Compiled information on the co-occurrence of anchovy larvae and zooplankton predators off California and Baja California for 1954, 1956, 1958 (Alvariño 1979, 1980 b) show that abundance of Medusae coincided with low number of absence of anchovy larvae.

Observations by Nagabushanam (1959) on the associations of young *G. merlangus* with the Scyphomedusae *Rhizostoma pulmo* (as *R. octopus*) indicated that 14 of 59 *G. merlangus* were in semi-digested stage, and he concluded that "they might have got into the stomach accidentally through rupture of the gastro-intestinal membrane". Another circumstance to consider is the regurgitation of food occurring in animals when disturbed by the trawling strain of the collecting nets, and the destruction of soft large medusae during the trawling operation.

Fraser (1969) detailed the feeding behavior of *Cyanea capillata* and roughly estimated the food consumption to provide an indication on the amount of food needed. He estimated that a small medusae 50 mm in diameter can capture 80 fish larvae in six and a half hours (indication of the importance of this feeding activity on recruitment of commercial fish stocks). Fraser (1969) observed the active voracity of *C. capillata* on the Amphipoda (*Gammarellus homarus*, *Calliopius laeviusculus*, *Parathemisto gaudichaudi*) Euphausiidae, Brachyuran zoeas, *Mytilus edulis*; 10.032 gr of *Temora*, and fish larvae; a 30 mm *C. capillata* consumed in 17 days, 500 specimens of *Temora*, 6 flat fish larvae, 12.5 to 15 mm in length, 3.34 gr of *Mytilus* meat; a 45 cm *Cyanea* weighting 6 Kg would require 3570 gr of wet weight food, about 166x 10^4 *Calanus*, which is equivalent to 15.000 fish larvae.

Fraser (1969) also notes that one *Melicertum costatum* consumed 36 fish larvae, 6 copepoda (*Temora*), and one piece of the medusae *Staurophora* in a period of 4 days. One *Leuckartiara nobilis* 17 mm in diameter consumed in 26 days, 22 fish larvae (yolk sac and post-yolk sac stages), 222 copepods (mostly *Temora*), 4 Amphipoda, 0.875 gr *Mytilus edulis*, 4 *Aglantha*, 1 *Sarsia*, 1 *Clione*, and pieces of *Staurophora*. *L. nobilis* uses its coiling and twisting tentacles to entangle fish larvae, copepods and large food items such as *Sarsia* and *Clione limacina* 25 mm long. Lebour (1922) observed a *L. octona* which ate young squid larger than itself, the squid "completely filled its (the medusae's) stomach and took several days to digest". The same specimen three days later caught two young *Cottus bubalis* at the same time it was catching another fish larvae with its tentacles. This species is highly voracious swallowing food larger than itself, and is "a dangerous species to keep in an aquarium, as it will eat almost anything and apparently is not much eaten by other animals "(Lebour 1923).

Staurophora mertensi the most abundant medusae in Logy Bay, ranges from 15 to 164 mm (90 to 120 mm is the most common size range). Fraser (1969) observed that the smallest specimen caught 8 post yolk sac fish larvae, which digested within 45 minutes, and in 4 days consumed 13 fish larvae, 47 copepods, 2 amphipods, and 0.1 gr *Mytilus*. Another specimen consumed within two weeks, 21 fish larvae. 200 copepods, 2 amphipoda, 2 zoeas, and 0.29 gr *Mytilus*.

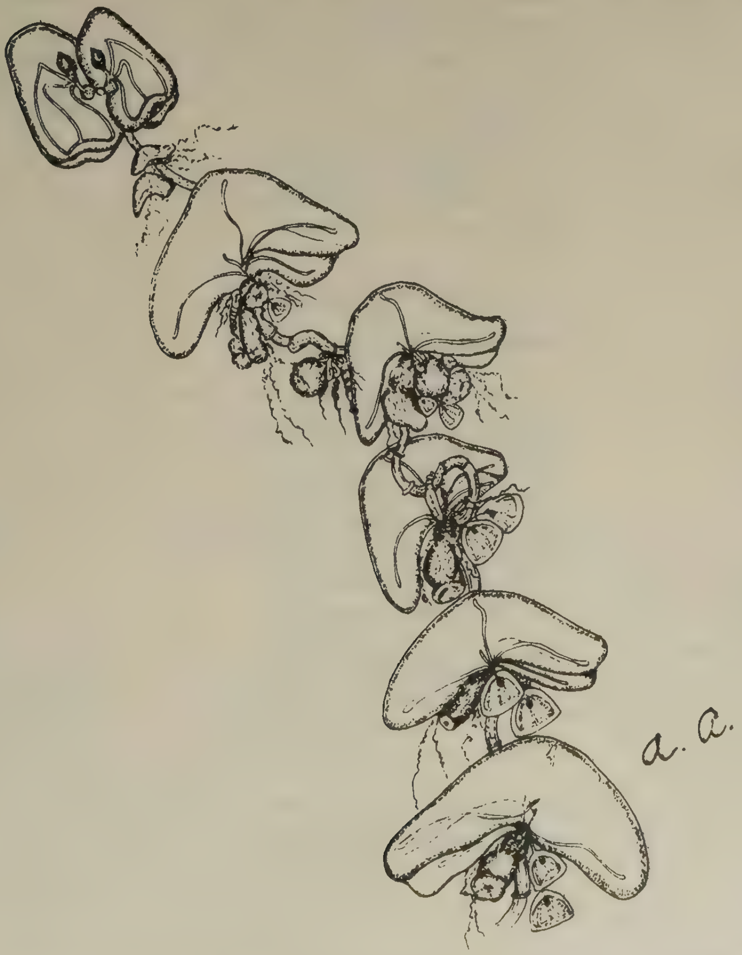
Fraser (1969) observed a small 5 mm *Boungainvillia superciliaris* catch 80 fish larvae in 6.5 hours, and noted a 10 mm diameter *Laodicea undulata* eat 5 fish larvae (inmediately post yolk sac) and 21 copepods, mainly *Temora*, within a 6-day period. He also saw small 7 mm diameter specimens of *L. undulata* from Logy Bay, constantly wiping the tentacles on the lips of the mouth to remove detritus, ciliates, and minute oil globules from *Coscinodiscus* (abundant in the plankton). This medusae swallowed, within a few minutes, *pandalid* larvae, euphausiid calyptopis, and *Calanus*.

Another medusae, *Tamoya haplonema* was observed feeding on small fish (Beebe 1928), and 4 *Chloroscombrus* (*Scombrus*) *chrysurus* fish, which had been killed with the powerful toxic nematocyst of the tentacles, were being draw into the mouth; at the same time, other fish had been trapped and were dying in convulsion in the water.

Chrysaora quinquecirrha also prefer fish as food; one specimen collected in the Travancore coastal waters of India, contained 239 fish larvae and young fish within the stomach (K. Nair 1947). I have observed *Chrysaora quinquecirrha* with *Trachurus trachurus* young invading the cavities of the medusae, which was already damaged and dying; and the fish took advantage of the situation seeking shelter and possibly also obtaining food.

Chiropsalmus quadrumanus is a Cubomedusae considered to be dangerous to humans as well as fish. Fish and Cobb (1954) believe it to be responsible for killing some swimmers.

There is a marker food selection and difference in catching ability in three large coelenterates, *Velella* and *Porpita* (Chondrophorae), and *Physalia* (Siphonophorae). These coelenterates appear in large dense patches at the surface of the oceans consuming fish eggs, larvae and young, and the eggs and various stages of the life cycle of other animals in the plankton inhabiting the surface waters of the oceanic domain. The food preferences of these two orders (Chondrophorae and Siphonophorae) are listed in Table II.



SIPHONOPHORAE *Nectocarmen antonioi* **Alvariño 1983**

TABLE 1. OBSERVATIONS ON THE FOOD OF MEDUSAE

Order: Family Species	Food	Author
ANTHOMEDUSAE: Corynidae		
Dipurena binicella Rees 1977	*Artemia*; epibenthic plankton	Rees, 1977
Sarsia tubulosa (M.Sars) 1835	*Hyperia* (Amphipoda)	Linko, 1900
	Acartia clausi, *Calanus finmarchicus*, *Temora longicornis* (Copepoda), and other Crustacea.	Lebour, 1922
	Copepoda, Decapod larvae	Lebour, 1923
	Small crustaceans	Fraser, 1969
	Clupea harengus (herring) larvae	Sveshnikov, 1963
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
Sarsia gemmifera Forbes 1848	*Calanus finmarchicus* (Copepoda)	Lebour, 1922
Sarsia prolifera Forbes 1949	*Labrus* sp. (larvae and juveniles); *Centropages typicus*, *C. finmarchicus* (Copepoda); Crustacea larvae; Annelid larvae; *Oikopleura* (Appendicularia)	Lebour, 1922
	Copepoda; Decapod larvae; other Crustacea	Lebour, 1923
Sarsia princeps (Haeckel) 1879	Copepoda	Fraser, 1969
: Tubulariidae		
Hybocodon prolifer L. Agassiz 1862	Eggs and larvae of Clupeidae and Ammodytidae; *Calanus*, *Acartia*, *Pseudocalanus*, *Temora* (Copepoda): Chaetognatha	Lebour, 1922
	Young *Sepia* (Cephalopoda)	McIntosh, 1926
Steenstrupia nutans (M.Sars) 1835	Fish eggs and larvae; *Temora longicornis*, *Corycaeus anglicus* (Copepoda); *Porcellanidae* larvae; *Gebia* larvae; Chaetognatha.	Lebour, 1922,1923
:Zancleidae		
Zanclea costata Gegenbaur 1856	Copepoda, Nauplii, and other zooplankters	Russell and Rees, 1936
:Cladonematidae		
Cladonema radiatum Dujardin 1843	Copepoda	Browne, 1900
C. californicum Hyman 1947	*Artemia*; fauna associated with *Zostera marina*	Rees, 1979
Eleutheria dichotoma Quatrefages 1842	*Harpacticus fulvus* (Tigriopus Copepoda)	Drzewina and Bohn, 1911, 1912, 1913
	Tigriopus, Copepoda	Fraser, 1969
:Rathkeidae		
Rathkea octopunctata (M.Sars) 1835	*Sardina pilchardus* larvae; *Pseudocalanus elongatus* (Copepoda): Crab zoea; *Poecilochaetus* larvae; other Crustacea larvae; *Oikopleura*	Lebour, 1922

Table 1. Cont.

Order: Family Species	Food	Author
	Herring and Sprat, Clupeidae larvae; Copepoda; Crustacea larvae; *Phialidium* and other Medusae, *Gebia* larvae; Chaetognatha; *Oikopleura* (Appendicularia)	Labour, 1923
	Synchaeta sp. (Rotifera)	Hollodway, 1947
	Fish larvae, even before the medusae were liberated from the hydroid	Fraser, 1969
Bougainvillidae		
Bougainvillia superciliaris (L. Agassiz) 1849	Copepoda; Chaetognatha	Hartlaub, 1897
	Fish larvae; Copepoda	Fraser, 1969
B. britannica (Forbes) 1841	*Ammodytes tobianus* larvae	Lebour, 1923
B. multitentaculata Foerster 1923	*Clupea pallasi* (herring) larvae	Arai and Hay, 198
Nemopsis bachei L. Agassiz 1849	Crustacea larvae; Dinoflagellates, and other plankters	Phillips et al, 1969
: Pandeidae		
Amphinema dinema (Péron and Lésueur) 1809	Copepoda; Chaetognatha	Hartlaub, 1897
	C. finmarchicus (Copepoda); Chaetognatha; *Cosmetira pilosella*, *Phialidium* sp. (Medusae); *Oikopleura* (Appendicularia)	Lebour, 1922
	Copepoda; Chaetognatha; 7 mm *Eutima gracilis* (Medusae)	Lebour, 1923
	fish larvae; Copepoda; Amphipoda; Medusae; Siphonophorae	Fraser, 1969
Leuckartiara octona (Fleming) 1823	*Nanomia cara* (Siphonophorae)	Mayer, 1910
	Cottus bubalis, *Blennius pholis* larvae; squids and other zooplankters	Lebour, 1922
	Gadus merlangus. *Cottus* sp., *Callionymus* sp. larvae; *Calanus*, *Acartia*, *Anomalocera* (Copepoda); *Podon* (Cladocera): *Poecilochaetus* larvae; *Gebia* larvae; Decapoda larvae, and other Crustacea	Lebour, 1923
	Ctenophora; other Medusae; Siphonophorae	Fraser, 1969
L. nobilis Hartlaub, 1913	Fish larvae; *Temora* (Copepoda); Amphipoda; *Clione limacina* (Pteropoda); *Sarsia*, *Aglantha* (Medusae)	Fraser, 1969
L. zacae Bigelow, 1949	Fish larvae	Alvariño (unpublished data)
Stomotoca atra L. Agassiz 1862	*Eperetmus typicus*, *Proboscidactyla flavicirrata*, *Aurelia aurita* (Medusae); *Pleurobrachia* (Ctenophora)	Arai and Jacobs 1980

Table 1. Cont.

Order: Family Species	Food	Author
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
: Calycopsidae		
Bythoriara stilbosa Mills and Rees, 1979	*Artemia*	Mills and Rees, 1979
LEPTOMEDUSAE: Melicertidae		
Melicertum octocostatum (M.Sars) 1853	*Polydora* (Polychaeta); Copepoda	Russell, 1953
	Larvae and young fish; *Temora* (Copepoda); *Staurophora* (Medusae)	Fraser, 1969
: Laodiceidae		
Laodicea undulata (Forbes and Goodsir) 1853	*Calanus* (Copepoda)	Lebour, 1922
	Blennius pholis larvae; Copepoda	Lebour, 1923
	Fish larvae; *Calanus*, *Temora* (Copepoda); Calyptopis Euphausiidae; *Pandalidae* larvae; other larvae	Fraser, 1969
Staurophora mertensi Brandt 1838	Copepoda; Annelida; Medusae	L. Agassiz 1849
	Calanus (Copepoda)	Bigelow, 1926
	Fish larvae; Copepoda; Amphipoda; other Crustacea and larvae; Mollusca	Fraser, 1969
:Mitrocomidae		
Cosmetira pilosella Forves 1848	*Lepadogaster gouani* larvae; *Caliqus rapax* (Copepoda); Crustacea larvae; Chaetognatha	Lebour, 1922
	Cottus, *Callionymus*, *Labrus* larvae; Copepoda; *Pleurobrachia* (Ctenophora); Chaetognatha	Lebour, 1923
Tiaropsis multicirrata (M.Sars) 1835	*Euphysa*, *Sarsia* (Medusae); other small animals	L. Agassiz, 1849
:Campanulariidae		
Obelia spp.	Fish larvae; Copepoda; Cladocera; Amphipoda; Ctenophora; Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1922
	Gadus merlangus, *Callionymus* sp. larvae; *Acartia*, *Paracalanus parvus*; *Pseudocalanus*, *C. finmarchicus* (Copepoda): *Gebia* larvae; Crustacea zoeas; *Podon*, *Evadne* (Cladocera); *Tomopteris helgolandica* and Annelida larvae; *Hybocodon*, *Obelia*, *Steenstrupia* (Medusae); *Oikopleura* (Appendicularia)	Lebour, 1923
Phialidium hemisphaericum (Linne) 1767	Fish larvae	Slabber, 1778
	Cottus bubalis, *Ammodytes tobianus*, *Agonus cataphractus*, *Solea vulgaris*, *Labrus bergylta*, *Gadus merlangus*, *G. minutus*, *Blennius pholis* larvae, and	

Table 1. Cont.

Order: Family Species	Food	Author
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
: Calycopsidae		
Bythoriara stilbosa Mills and Rees, 1979	*Artemia*	Mills and Rees, 1979
LEPTOMEDUSAE: Melicertidae		
Melicertum octocostatum (M.Sars) 1853	*Polydora* (Polychaeta); Copepoda	Russell, 1953
	Larvae and young fish; *Temora* (Copepoda); *Staurophora* (Medusae)	Fraser, 1969
: Laodiceidae		
Laodicea undulata (Forbes and Goodsir) 1853	*Calanus* (Copepoda)	Lebour, 1922
	Blennius pholis larvae; Copepoda	Lebour, 1923
	Fish larvae; *Calanus*, *Temora* (Copepoda); Calyptopis Euphausiidae; *Pandalidae* larvae; other larvae	Fraser, 1969
Staurophora mertensi Brandt 1838	Copepoda; Annelida; Medusae	L. Agassiz 1849
	Calanus (Copepoda)	Bigelow, 1926
	Fish larvae; Copepoda; Amphipoda; other Crustacea and larvae; Mollusca	Fraser, 1969
:Mitrocomidae		
Cosmetira pilosella Forves 1848	*Lepadogaster gouani* larvae; *Caliqus rapax* (Copepoda); Crustacea larvae; Chaetognatha	Lebour, 1922
	Cottus, *Callionymus*, *Labrus* larvae; Copepoda; *Pleurobrachia* (Ctenophora); Chaetognatha	Lebour, 1923
Tiaropsis multicirrata (M.Sars) 1835	*Euphysa*, *Sarsia* (Medusae); other small animals	L. Agassiz, 1849
:Campanulariidae		
Obelia spp.	Fish larvae; Copepoda; Cladocera; Amphipoda; Ctenophora; Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1922
	Gadus merlangus, *Callionymus* sp. larvae; *Acartia*, *Paracalanus parvus*; *Pseudocalanus*, *C. finmarchicus* (Copepoda): *Gebia* larvae; Crustacea zoeas; *Podon*, *Evadne* (Cladocera); *Tomopteris helgolandica* and Annelida larvae; *Hybocodon*, *Obelia*, *Steenstrupia* (Medusae); *Oikopleura* (Appendicularia)	Lebour, 1923
Phialidium hemisphacricum (Linne) 1767	Fish larvae	Slabber, 1778
	Cottus bubalis, *Ammodytes tobianus*, *Agonus cataphractus*, *Solea vulgaris*, *Labrus bergylta*, *Gadus merlangus*, *G. minutus*, *Blennius pholis* larvae, and	

Table 1. Cont.

Order: Family Species	Food	Author
	eggs of *Onos* and *Gobius*; *Acartia clausi*, *C. finmarchicus*, *Temora longicornis*, *Pseudocalanus elongatus* (Copepoda); nauplii of Cirripedia; *Pandalus*, *Porcellana* larvae; *Carcinus maenas* zoeas, *Gebia* larvae and other Crustacea; *Hypolite* and *Spionid* larvae (Polychaeta); *Obelia*, *Cosmetira pilosella*, *Phialidium* (Medusae); *Muggiaea* (Siphonophorae), Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1922
	Cottus, *Onos*, *Labrus*, *Clupea harengus* larvae; *Pseudocalanus*, *Centropages typicus*, *Calanus* (Copepoda); *Gebia* *Porcellana* larvae, crab zoeas (Crustacea); *Rathkea*, *Obelia*, *Amphinema* (Medusae); Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1923
	Fish larvae; Euphausiidae; Copepoda; Onvertebrate larvae; Appendicularia	Bigelow, 1926
	Herring and other fish larvae	Fish, 1932 (i Gudger, 1937)
	Preference of fish larvae over Copepoda	Fraser, 1969
Phialidium gregarium (L.Agassiz) 1862	Herbivorous zooplankters	Huntley and Hobson, 1978
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
:Eutimidae		
Eutima gracilis (Forbes and Goodsir) 1853	*Gebia* larvae	Lebour, 1922
	Fish larvae; Copopoda; *Obelia* Medusae); Chaetognatha	Lebour, 1923
	Other Medusae	Fraser, 1969
Tima formosa L. Agassiz 1862	Ammodytidae larvae and young	Fish 1924 (in Gudger, 1937)
Eutonina indicans (Romanes 1876	*Sarsia*, *Aurelia aurita* (Medusae); *Pleurobrachia* (Ctenophora)	Arai and Jacobs, 1980
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
Aequoreidae		
Aequorea sp.	*Lepadogaster*, *Blennius pholis*, pipefish larvae and young; *Palaemon* and other Crustacea larvae; *Pleaurobrachia* (Ctenophora)	Lebour, 1923
	Eggs and fish larvae	Lee, 1966
	Bolinopsis (Ctenophora); *Salpa cylindrica* and other salps (Tunicates)	Hamner et al, 1975
Aequorea victoria (Murbach and Shearer) 1902	*Artemia salina*, other Crustacea; *Sarsia*, *Phialidium gregarium*, *Aurelia*	

Table 1, Cont.

Order: Family Species	Food	Author
	(Medusae); *Pleurobrachia* (Ctenophora)	Arai, 1980 Arai and Jacobs, 1980
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
LIMNOMEDUSAE: Olindidae		
Aglauropsis aeora Mills, Rees and Hand, 1976	*Artemia*	Mills, Rees and Hand, 1976
Gosea corynectes (Gosse) 1853	Crab zoeas (Crustacea)	Russell, 1953
Craspedacusta sowerbyi Lankester 1880	Gold fish	Schmitt, 1939
	Young fish	Kramp, 1950
	Daphnia and other Crustacea; Rotifera; Protozoa	Rusell, 1953
Gonionemus vertens A. Agassiz 1862	Young fish	C.W. Hargitt, 1905 a, b Perkins (in Gudger, 1937)
	Siphonophorae; Ctenophora; other Medusae	Fraser, 1969
:Proboscidactylidae		
Proboscidactyla stellata (Forbes) 1846	Chaetognatha	Lebour, 1923
P. flavicirrata Brandt 1853	Small Cyclopoid and Copepoda nauplii; *Artemia*; Cladocera Trocophora larvae; crab zoea; eggs	Spencer, 1975 Rees, 1979
TRACHYMEDUSAE: Geryonia		
Liriope tetraphylla (Chamisso and Eysenhardt) 1821	Fish larvae and young fish	McCrady, 1858
	Fish larvae	Fraser, 1969
:Ptychogastriidae		
Tesserogastria musculosa Beyer 1959	Harpacticoid Copepoda; small Crustacea	Hesthagen, 1971
:Rhopalonematidae		
Aglantha digitale (O. F. Muller) 1776	*Calanus finmarchicus* (Copepoda)	Lebour, 1922
	Oithona similis, *Oncaea borealis* and other Copepoda; *Polydora* larvae; Gastropod larvae; Lamellibranch larvae; eggs of invertebrates; *Noctiluca* (Dinoflagellate)	Smedstad, 1972
PTEROMEDUSAE		
Tetraplatia volitans Busch 1851	Crustacea; Annelid larvae; Chaetognatha	Dantan, 1925

Table 1, Cont.

Order: Family Species	Food	Author
	Copepoda; young Euphausiidae; Chaetognatha	Hand, 1955
STAUROMEDUSAE: Eleutherocarpidae		
Kishinouyea corbini Larson 1980	Small shrimps; *Hippolyte* and Gammparids; Amphipoda	Larson, 1980
CUBOMEDUSAE: Carybdeidae		
Carybdea marsupialis (Linnaeus) 1758	Young fish	Conant, 1897
	Larval and young fish, *Acartia* (Copepoda); Stomatopod larvae; Isopoda; *Ceratonereis* (Polychaeta): Chaetognatha	Berger, 1900; Larson, 1976
Carybdea alata Reynaud, 1830	Mysidacea; crab megalopa; Polychaeta	Larson, 1976
C. rastoni Haacke 1886	Fish larvae and juveniles; Mysidacea; Polychaeta	Uchida, 1929 Ishida, 1936 Gladfelter, 1973 Larson, 1976
Tamoya haplonema Müller, 1859	*Chloroscombrus chrysurus* larvae	Beebe, 1928
Tripedalia cystophora Conant 1897	*Oithona* (Copepoda)	Larson, 1976
:Chirodropidae		
Chiropsalmus quadrumanus (Müller) 1859	Young fish	Hyman, 1940
	Squilla, *Lucifer* spp., other Crustacea larvae; crab zoeas; Amphipoda	Phillips and BURKE, 1970
	Fish larvae; Amphipoda; Cumacea; Stomatopoda; *Lucifer*, crabs and other Crustacea larvae	Phillips et al. 1969 Larson, 1976
Ch. quadrigatus Haeckel 1880		
Chironex fleckeri Southcott 1956	Fish; Caridean and other Crustacea	Barnes, 1966
CORONATAE: Linuchidae		
Linuche unguiculata (Schwartz) 1788	Young fish	Beebe, 1928
:Periphyllidae		
Periphylla periphylla (Perón and Lésueur) 1809	Young Myctophidae fish	Clarke and Herring 1969
SEMAEOSTOMEAE: Pelagidae		
Chrysaora sp.	Fish larvae; Copepoda; *Tomopteris* (Polychaeta); *Leuckartiana* (Medusae); *Beroë* (Ctenophora); Siphonophorae; Chaetognatha	Delap, 1901

Table 1, Cont.

Order: Family Species	Food	Author
	Fish larvae	Lebour, 1922
	Ctenophora	McNamara, 1955
	Fish egg and larvae	Lee, 1966
Chrysaora hysoscella (Linnaeus) 1766	Coelenterata	Delap, 1901
	Cottus, *Blennius*, *Gobius*, *Lepidogaster* larvae; Copepoda; Decapoda larvae; *Phialidium*, *Cosmetira*, *Amphinema*, *Obelia*, *Aurelia* (Medusae); *Pleurobrachia* (Ctenophora); *Tomopteris* (Polychaeta); Chaetognatha	Lebour, 1923
	Fish larvae; Copepoda; Amphipoda; Siphonophorae; other Medusae; Ctenophora	Fraser, 1969
Ch. quinquecirrha (Desor) 1848	Clupeidae young fish	A. Agassiz, 1865
	Larvae and young fish	K. Mair, 1947
	Peprilus triacanthus young fish	Mansueti, 1963
	Shrimp Crustacea; *Mnemiopsis leidyi* (Ctenophora); Polychaeta	Cargo and Schultz 1966, 1967
	Cyprinodon variegatus, *Mugil cephalus*, *Oligoplites saurus* larvae and juveniles; small Crustacea and larvae; *Mnemiopsis mccradyi* (Ctenophora)	Phillips et 1969
	Mnemiopsis leidyi, *Beroë ovata* (Ctenophora)	Miller, 1974
	Mnemiopsis leidyi (Ctenophora)	Burrell and van Engel, 1976
Small *Pelagidae* *Pelagia* sp.	Fish eggs	Oesterbol, 1885
	Obelia and other Hydromedusae; *Thalia democratica* (Tunicata)	Delap, 1907
:Cyaneidae		
Cyanea capillata (Linnaeus) 1758	Young fish; *Nereids* Annelida	Gaede,1816
	Young fish and larvae	C. W. Hargitt, 1902 1905 a, 1905 b Bartels, 1910
	Copepoda; Medusa planula; Echinoderm larvae	C. W. and G. T. Hargitt, 1910
	Copepoda and other zooplankters	Bigelow, 1926
	Crustacea; Hydromedusae; Ctenophora	Hagmeir, 1933
	Obelia (Medusae)	Russell, 1953
	Ctenophora	Cargo and Schultz 1967
	Fish larvae; *Temora* (Copepoda); *Parathemisto gaudichaude* (Amphipoda); *Gammarellus homarus*, *Calliopius laevisculus* (Crustacea); Brachyura zoeas; *Mytilus* (Mollusca)	Fraser, 1969

Table 1, Cont.

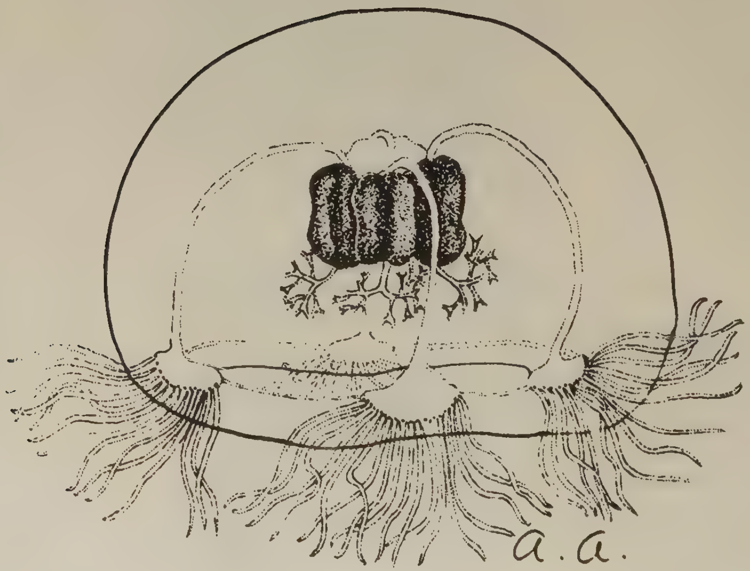
Order: Family Species	Food	Author
	Ctenophora	Phillips et at. 1969
	Artemia and small plankton	Cargo, 1975
C. lamarcki Perón and Lésueur 1809	Fish eggs; Copepoda; *Pleurobrachia*, *Beroë*, *Bolina* (Ctenophora); *Obelia*, *Phialidium*, *Cosmetira*, *Laodicea*, *Steenstrupia* (Medusae)	Delap, 1905
C. purpurea Kishinouye 1910	Young fish	K. Nair, 1947
:Ulmaridae		
Aurelia aurita (Linnaeus) 1758	Sea scorpio young fish	Fabricius, 1780
	Young fish	Spallanzani, 1793 C. W. Hargitt, 1905 a, 1905 b
	Copepoda; Ctenophora; *Obelia*, *Phialidium* (Medusae); Pteropoda	Delap, 1907
	Ammodytes tobianus, *Cottus bubalis*, *Agonus cataphractus*, *Solea vulgaris*, *Gobius minutus*, *Blennius pholis*, *Nerophis lumbriciformis* larvae; Amphipoda; crab zoeas; Decapoda and Mollusca larvae	Lebour, 1922
	Young fish; *Calanus*, *Harpacticoid* (Copepoda); *Balanus* and other Cirripedia larvae; Crustacea larvae; Oyster larvae; *Crepidula* larvae; Gastropoda larvae; young Polychaeta; Nematoda; *Epicarium* larvae; *Polydora*; Ascidian; Tintinnidae; Rotifera; Diatomacea	Orton, 1922
	Cottus bubalis, *Gadus pollachius*, *Syngnatus acus*, Flat fish, Clupeidae larvae; *Acartia clausi*, *Centropages typicus*, Harpacticoids (Copepoda); Decapoda larvae; Mollusca larvae; *Rathkea octopunctata*, *Phialidium* sp. (Medusae)	Lebour, 1923
	Fish larvae; Copepoda; Euphausiidae; other invertebrate larvae; Appendicularia	Bigelow, 1926
	Fish larvae	Fish, 1926 (in Gudger, 1937)
	Plaice larvae; Copepoda	Southward, 1955
	Nereids; Gammarids; *Balanus balanoides* larvae; spiders, Insects; *Corophium*	Hüsing, 1956
Aurelia aurita (Linnaus) 1758	*Coscinodiscus jonesianus*, *C. janischii*, *Thalassionema nitzschoides*, *Cyclotella caspia*, *Rhizosolenia calcaravis*, *Melosira sulcata* (Diatoms); *Ceratium furca*, *Prorocentrum micans*, *Peridinium steinii* (Dinoflagellates); *Ebria tripartita*, *Pontosphaera huxley* (Cocolitophorida); *Anomalocera*	

Table 1, Cont.

Order: Family Species	Food	Author
	patersoni, *Paracalanus parvus*, *Oithona nana* (Copepoda); *Sagitta setosa* (Chaetognatha); Decapod Crustacea larvae; Cirripedia Cypris; *Oikopleura dioica* (Appendicularia)	Milhailov, 1962
	Fish eggs and larvae; *Tigriopus* (Copepoda); Crustacea larvae; *Noctiluca*; Ciliates; Diatomacea	Lee, 1966
	Calanus glacialis, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia longiremis*, *Oithona similis*, *Oncaea borealis*, *Cyclopina* sp., *Harpacticus uniremis*, *Microsetella norvegica*, *Tisbe furcata* (Copepoda); *Balanus balanoides* nauplii and cypris (Cirripedia); Gastropoda and Bivalvia larvae; *Podon leuckarti*, *Evadne nordmanni* (Cladocera; *Sagitta elegans* (Chaetognatha); *Ophiopluteus* and Bipinnaria larvae (Echinodermata); Polychaeta larvae; *Beroë cucumis*, *Bolinopsis infundibulum* (Ctenophora); *Obelia* sp., *Rathkea octopunctata*, *Coryne tubulosa*, *Bougainvillia superciliaris* (Medusae); *Oikopleura vanhoffeni*, *Fritillaria borealis* (Appendicularia); *Tintinopsis campanula*, *Parafavella gigantea*, *Helicostomella subulata* (Tintinoidea)	Longinova and Perzova, 1967
	Ammodytes, *Gadus callarias*, *G. minutus* larvae; Copepoda; Amphipoda; Decapoda larvae; other medusae; *Mytilus* (Mollusca)	Fraser, 1969
Aurelia aurita (Linnaeus) 1758	*Artemia*	Cargo, 1975
	Fish larvae; Copepoda	Möller, 1979
	Obelia sp., *Rathkea octopunctata*, *Laodicea*, *Phialidium*, *Sarsia* (Medusae); *Pleurobrachia* (Ctenophora)	Arai and Jacobs, 1980
	Clupea harengus, *Cottus* larvae; Hydromedusae, *Aurelia* ephyra; Copepoda; Cladocera; Amphipoda; Cumacea	Möller, 1980
	Clupea harengus (herring) larvae	Moeller, 1982, 1983 Bailey and Bathy 1983
RHIZOSTOMEAE: Cassiopeidae		
Cassiopea frondosa (Pallas) 1774	Young fish; Crustacea; Mollusca	H.G. Smith, 1936
:Catostylidae		
Cambrionella orsini (Vanhoffen) 1888	Young fish	K. Nair, 1947

Table 1, Cont.

Order: Family Species	Food	Author
:Rhizostomatidae		
Rhizostoma octopus (Linnaeus) 1758	Larvae and young fish; Copepoda; Isopoda; other Crustacea and their larvae; Polychaeta larvae; Chaetognatha	Hamann, 1881
:Stomolophidae		
Stomolophus maleagris L. Agassiz 1862	Small plankton	Phillips et al., 1969



MEDUSAE: *Bougainvillia principis* **(Steenstrup) 1850**

CHONDROPHORAE

The Order Chondrophorae includes organisms inhabiting the- Uppermost oceanic layers at the air-water interface. These voracious animals feed on fish eggs and larvae, and the larvae - and adults of other zooplanketers. Data on the food of Chondrophorae include only two genera, *Porpita* and *Valella.*

Porpita, with no sail or propulsion mechanism, drifts with the waters, and relies largely on the muscular movements of its dactilozoids (Mackie 1959) to capture the food. It can detect vibrations in the waters (Horridge 1966), and is thus able to grab actively swimming animals. Large *Porpita* catch food by the medusae-bearing appendages (Bieri 1970) and the central - oral chamber ingests most of the food in the small ones. *Porpita* shows great ability to catch active copepods and a *Porpita* 5.5 mm in diameter is able to eat adult *Pontellid* copepods as big as itself.

Porpita catching large, fully mature carnivorous copepods (Bieri 1970) could be an example of a predator attempting to attack *Porpita* but being eaten themselves. *Porpita* would in - this case be a secondary carnivore. Analysis of the food of - *Porpitas* washed up on the beaches of Shirahama, Japan, in November 1965 (Bieri 1970) consisted of carnivorous Calanoid copepods (90% of the diet), together with crab megalopas, fish larvae and fish eggs (10%), as well as Gastropoda veligers, Lucifer, Larvaceans, Medusae, and Nematodes.

The wind-driven *Velella* sails through the water, offering minimum resistence to movement because it has no tentacles; the dactilozoids are of oval cross section with nematocyst bands on their narrow edges. *Velella* feeding is mainly passive; the animal drifts along the waters at the vein of the blowing wind, and captures zooplankters and eggs of fish and other animals inhabiting the uppermost layers of the ocean in the *Velella's* sailing path.

Velella do not appear to catch motile organisms such as - fish larvae, copepods and nauplii, as effectively as the weak swimming zooplankters, larvaceans or the non motile eggs of fish and invertebrates, although comparatively large and active organisms, such as fish larvae and adult Euphausiidae are - - occasionally caught. In studying the post-larval food of *Velella lata* obtained off San Diego, California Bieri (1961) found that in 99 specimens collected on May 1950, fish eggs, mostly of *Trachurus symmetricus* (jack mackerel) made up 48% of the total food count, and euphausiid eggs 7%; in 36 specimens collected in March 1954, euphausiid eggs made up 78% of the food - - items, and fish eggs 3%. Huxley (1858) found Copepoda remains in the gastrozoids of *Velella lata* Chamisso and Eysenhardy 1821. Lebour (1947) observed the stomachs of *Velella* from Valencia, Ireland, filled with Harpacticoid copepods, and Totton (1954) observed Copepoda and crustacea remains. From the data available, it appears that fish eggs and euphausiid eggs make up a large portion of *Velella's* diet. Variations in the food type observed correspond to the populations which *Velella* encounters, while through a region. If the prey animals escape, *Velella* cannot purse them.

Velella is a recognized conspicuous carnivorous feeder, - eating any organism ranging in size from 0.2 mm to 10 mm or more. The amount of food intake increases with the size of *Velella*; Bieri (1961) noted that the amount of Calanoid copepods caught by *Velella* increases with the size of the *Velella* when these are greater than 30 mm in length. In these cases, *Velella* appeared with digested and semidigested animals in the gastrozoids and siphons; fish egg and larvae, primarily *Engraulis mordax* (northern anchovy) and *Cololabis saira* (saury), Chaetognatha and - their eggs, barnacle nauplii (probably of *Lepas*) Siphonophorae, Crustacea Decapoda larvae, Mysids, Copepoda (eggs, larvae and adults), Euphausiidae (eggs, larvae and adults), Pteropoda, AmPhipoda, Cladocera, *Emerita* larvae and the Diatom *Coscinodiscus*. The seasonal occurrence of *Velella* off California (Bieri 1961) is closely related with the spring spawning of *Merluccius productus*, *Cololabis saira*, *Sardinops Caerulea*, and *Trachurus symmetricus*. I have observed large quantities of *Velella* in the Peru Current region off Peru, in 1968, feeding on *Engraulis ringens* (anchovy) eggs and larvae, Copepoda, and other fish larvae.

SIPHONOPHORAE

Relatively little has been published on the feeding habits of siphonophores. They are planktonic animals which are difficult to maintain in the laboratory due to the large size of some species, and their general excitability and autotomy; yet, under adequate conditions, they have been maintained in laboratory aquaria for some weeks, feeding, growing, reaching sexual maturity, and reproducing. Under these conditions, their feeding and excitable behavior have been closely observed, and they have been found to be rapacious predators (Alvariño 1967a).

Siphonophores occur primarily in temperature and warm oceanic waters, where they feed on fish larvae and young fish, as well as competing for food with young and adult fish and other pelagic animals. Siphonophores possess anatomical structures ideally suited for "fishing" purposes; their tentacles containing poisonous nematocysts, glide through the waters like fishing lines, luring even with mimicry (Purcell 1980) the fish into a deadly trap. Siphonophores swim swiftly and their transparent bodies are not easily detected by their victims. Observations on the searching action of the gastrozoids indicate their activity is due to tactic and chemical excitability - (Mackie and Boag 1963); nematocysts are located in the tentacles, tentilla, and also around the oral region.

Siphonophorae ingest countless number of Copepoda and - other zooplankters (Bigelow 1926), but feed primarily on fish larvae when available. Analysis of zooplankton of the Bombay region during 1944 to 1947 showed (Bal and Pradhan 1952) that the highest number of siphonophores coincided with a minimum of fish larvae and post larval stages, and high numbers of hydromedusae and siphonophores in 1947 coincided with the lowest number of fish larvae. Unfortunately, published observations on the food of siphonophores include only a few of the approximately 140 species in the group.

The Cystonectae *Epibulia ritteriana* Haeckel 1888 is a surface-floating organism which is seldom captured by plankton hauls, primarily because this stratum is almost never sampled by plankton tows (Alvariño 1972). Therefore, the scarcity of *E. ritteriana* is probably only apparent. Thus cystonect feeds voraciously on epiplanktonic animals, primarily those inhabiting the uppermost layers of the oceans, Clupeidae, Engraulidae and other fish larvae and animals eventually reaching the - neuston or pleustonic epiplanktonic domain. The tentacles of this Cystonectae may reach 80 to 200 mm or more when fully extended through the waters like fishing lines, with the gastrozoids actively searching for food. I have observed *E. ritteriana* with remains of Clupeidae and the eyes of Myctophid inside the gastrozoids. Some authors indicate photophores on *E. ritteriana* siphons and gastrozoids, while others disagreed on this. I observed that photophores inside the gastrozoids of *E. ritteriana* belong to the Myctophids the siphonophore has been feeding on.

The Cystonectae *Physalia physalis* (Portuguese-Man-of-War), catches fish (larvae, young and adults) swimming or floating near the surface of the oceans (Gudger 1942). This siphonophore has long, delicate, and almost transparent tentacles 8-10 meters long. These tentacles are covered with deadly neeling poisonous cells and cnidoblasts, which sting and poison young fish; the prey is later drawn and digested by the gastrozoids. Mackie and Boag (1963) observed that *Physalia* shortens its tentacles by coiling and contracting them to 12-15 cm in lenght during their feeding, an observation which was further corroborated by Bieri (1970).

The feeding behaviour of *P. physalis* has been described in detail by Wilson (1947) from specimens maintained in a tank in the Marine Laboratory at Plymouth, England, and found *Physalia* feed on young and small fish. This Cystonectae first would sting the fish with the poisonous dactylozoids and then the gastrozoids would actively cover the fish and ingest it.

Totton (1960) indicated that *P. physalis* is apparently - very successful in avoiding being devoured, except in the juvenile stage, and that surface swimming fish (Trachuridae, Exocetidae and others) become entagled by the tentacles of *Physalia*, obtaining more food than can digest.

Physalia physalis inhabit warm waters, and during some seasons and years they appear in great abundance; this happens in the Portuguese coastal areas; reaching northward to the British Isles. They are found similary along the Atlantic coasts of North America.

Physonectae siphonophores feed on small fish and crustaceans (Hardy 1956). Observations on *Nanomia cara* specimens - kept alive (Mackie and Boag 1963) for 36 days at Friday Harbor show that they swim by contractions of the nectophores; and changes in the vertical displacements are controlled by adjustment of the volume of CO inside the pneumatophore. When the specimens were fed with small crustaceans (*Artemia* nauplii, *Tigriopus*, etc.) and pieces of fresh meat, it was observed that their need for food was indicated by the state of expansion of palpons; and also, when the palpons were filled with a milky fluid, no food was necessary. Siphonophores react to stimulation by a sudden swimming action at the speed of 8 cm per second, with a contraction of the nectophores 4 times per second, at 16°C temperature. Barham (1966) observed a mixed population of Physonectes, mainly *Stephanomia bijuga* extending above the

Myctophids layers, their migratory descent to deep layers was more rapid in the physonectes than in the Mytophids.

The feeding behavior of several other physonectae have described *Physophora hydrostatica* by Hardy (1956), with upward-jerks-like contraction of elastic fibers made by the tentacles in order to carry small crustaceans to the mouth of gastrozoid. *Ph. hydrostatica* may appear to be quietly floating, while all its tentacles are extended like fishing lines. At other times it will swim actively, with tentacles and tentilla contracted, offering the least resistance to movements, as it swiftly moves towards a more adequate field of feeding operations.

Stephanomia bijuga was observed by Barham (1963) motionless in a "feeding position with the tentacles stretched out in all directions. "These active predatory animals create a living net formed by living fishing lines, apreading across the world oceans. They are able to sink to deep layers expelling gas from the Pneumatophore, reduce their body area by contraction of the stem, tentacles and tentilles, and perform rapid movements, swimming to the upper oceanic layers by "expansion of the gas within the pneumatophore". Berril (1930) described the behavior of *S. bijuga*, explaining that "unless disturbed" the specimens remain perfectly motionless in an inclined position, with the pneumatophore and nectosome part of the stem in a vertical position, and the scyphosoma part of the stem falling out "at an angle of about forty five degrees". In this manner the tentacles and tentille hang separately and are spaced to form an efficient trap, drifting with the current and catching small active zooplankters. For example, the Physonect *Stephanomia rubra* reach 150 cm of total length and the extended tentacles up to 750 cm. Contact of any small organism with a filament or tentacle triggers the instantaneous discharge of dactylozoids, and contraction of the tentacles, and a searching activity of the associated gastrozoids. Gastrozoids of *Forskalia edwardsi* were observed to contain fish of more than 25 mm in length (Leuckart 1853) which were digested up to the skelton.

Duvault (1965) studied the feeding reaction in siphonophore Calcycophorae, which paralize their prey by the discharge of nematocysts, followed by contraction of the tentacles and dilatation of the mouth of gastrozoids. These animals move through the water in an ondulatory fashion (Hardy 1956) powered by the jet propulsion of the swimming bells; and in time of danger the scyphosoma is quickly retracted into the shelter of the hydroecium of the nectophore. Observations on the small Calcycophorae *Muggiaea atlantica* conducted at Friday Harbor (Mackie and - Boag 1963) revealed that, the specialized type of swimming and spreading behavior of the tentacles is quite different from that occurring in the Physonectes. The nectophore performs rapid movements in spiral loop fashion; the tentacles are thus spread - out simultaneously in a centrifugal sequence, in the manner of the bullfighter "veronica". It is a technique of combing the water in swirls, by which a good number of victims are captured by the siphonophore and the prey are transferred from the tentacles to the mouth of adjacent gastrozoids. I have observed the small *Muggiaea atlantica* with the tentacles spread reaching 25 mm long.

Parasites which appear in siphonophores may be related to the prey they are feeding on. Dollfus (1963) cited observations by T. Studer (1878) on a Tetraphyllidear like protocercoid observed in the float cavity of the Physonectae *Agalma* sp., and Totton (1954) described a specimen of *Hippopodius hippopus* from Villefranche-sur-Mer, with 50 *Trichocercous* cercaria (with eyes) probably the larval stage (*Cercaria setigera* Monticelly) of the trematode *Lepocraedium album* Stossich. These parasites made tubular tunnels into the mesoglea of *H. hippopus*, lost their tail, and *H. hippopus* may obtained the parasites by feeding on fish.

TABLE II. OBSERVATIONS ON THE FOOD OF COELENTERATES

ORDER/SUBORDER: Family Species	Food	Author
CHONDROPHORAE: Porpitidae		
Porpita sp.	Eggs, larvae and juvenile fish; carnivorous *Calanoid* Copepoda; Medusae; *Lucifer*; Gastropoda larvae; Nematoda	Bieri, 1970
: Velellidae		
Velella sp.	Harpacticoid Copepoda	Lebour, 1947
	Fish eggs; small Crustacea larvae	Bieri, 1970
Velella lata Chamisso and Eysenhardt 1821	Copepoda	Huxley, 1858
	Calanoid Copepoda	Totton, 1954
	Fish eggs and larvae; larval and adult Copepoda; Euphausiidae; Amphipoda; Cladocera; *Barnacle* nauplii, and other Crustacea larvae; Chaetognatha; Diatomacea	Bieri, 1961
	Angraulis ringens larvae and eggs	Alvariño (Unpublished data)
SIPHONOPHORAE		
Suborder CYSTONECTIDAE: Epibulidae		
Epibulia ritteriana Haeckel 1888	Young fish	Alvariño, 1972
	Engraulidae, Clupeidae, Myctophidae, Scomberesocidae larvae and young fish	Alvariño (unpublished data)
: Rhizophysidae		
Bathyphysa sibogae Lens and van Riemsdijk 1908	Associated Hyperid Amphipoda *Schizoscelus ornatus*, *Thyropus edwardsii*	Biggs and Harbison 1976
	Fish larvae	Purcell, 1981a
Rhizophysa filiformis (Forskal) 1775	Small fish; Alcyopid Polychaeta	Biggs, 1977
R. eysenhardti Gegenbaur 1859	Fish larvae	Purcell, 1981a
: Physalidae		
Physalia physalis Linn 1858	Herring, flying fish and other	Lesson, 1843; Quatrefages, 1854 Bigelow, 1891
	Centronotus ingerfish	Bennet (Gudger 1942)
	Young fish	Gudger, 1942
	Ctenolabrus rupestris	Wilson, 1947

TABLE II. Cont.

ORDER/SUBORDER: Family Species	Food	Author
	young and small fish	Totton, 1960; Mackie and Boag, 1963; Bieri, 1970
Suborder PHYSONECTAE: Agalmidae		
Nanomia cara Agassiz 1865	*Artemia* nauplii; *Tigriopus* (Copepoda)	Mackie and Boag, 1963
	Euphausiidae	Rogers, Biggs and Cooper, 1978.
Agalma okeni Eschscholtz 1825	*Acartia*, *Pleuromamma* (Copepoda) *Leander tenuicornis*, crab megalopa, *Artemia* and other Crustacea	Biggs, 1976
	Parathemisto (Amphipoda)	Biggs, 1977
	Crab megalopa, large Copepoda; Euphausiids	Purcell, 1980
Agalma elegans Sars 1846	Megalopa larvae	Biggs, 1977
Stephanomia bijuga (Chiaje) 1841	Mysidacea	Biggs, 1977
	Euphausiidae	Alvariño (unpublished data)
Stephanomia rubra Vogt 1852	Copepoda	Alvariño (unpublished data)
:Athorybiidae		
Athorybia rosacea Forskal 1775	Small fish; *Lucifer typis* (Sergestidae); Hyperidae Amphipoda; *Candacia*, *Corycaeus* (Copepoda); Polychaeta	Biggs, 1977
	Fish larvae; Shrimp larvae; Chaetognatha	Purcell, 1980
: Physophoridae		
Physophora hydrostatica Forskal 1775	Crustacea	Hardy, 1956
: Forskaliidae		
Forskalia edwardsi Kölliker 1853	Young fish Stomatopod larvae	Leuckart, 1853 Biggs, 1977
Forskalia tholoides Haeckel 1888	Small fish; *Anchylomera blossevillei*, *Hemityphis rapax* (Amphipoda); *Candacia* (Copepoda); Polychaeta; Heteropoda	Biggs, 1977
Suborder CALYCOPHORAE: Prayidae		
Rosacea cymbiformis (Chiaje) 1822	*Corycaeus*, *Candacia* (Copepoda)	

TABLE II. Cont.

ORDER/SUBORDER: Family Species	Food	Author
	Gastropoda veliger	Biggs, 1977
	Fish larvae; crab zoea and megalopa larvae; *Lucifer* and other Segestids; Polychaeta; *Creseis* sp. (Pteropoda); Atlanta sp. (Heteropoda); clam veligers and Gastropod veligers; juvenile shrimps; Mysids; *Sagitta enflata* (Chaetognatha); *Labidocera acutifrons*, *Pontellopsis lubbochi*, *Candacia curta*, *Oncaeca venusta*, *Oncaea media*, *Acrocalanus longicornis*, *Eucalanus attenuatus*, *Labidocera acuta*, *Paracalanus parvus*, *Scolecith danae*, *Temora discaudata*, *Corycaeus catus*, *Corycaeus* sp., *Farranula gibbula*, *Oithona plumifera*, *Clytemnestra rostrata* (Copepoda)	Purcell, 1981b
Stephanophyes superba Chun 1891	*Candacia* (Copepoda); Euphausiidae	Biggs, 1977
: Diphyidae		
Sphaeronectes gracilis (Claus) 1873	Copepoda	Purcell and Kreme 1983
Sulculeolaria monoica Chun 1888	*Candacia* (Copepoda)	Biggs, 1977
Muggiaea atlantica Cunningham 1892	Clupeidae larvae; small Copepoda	Alvariño 1979. 1980a, 1980b
Chelophyes appendiculata Eschscholtz 1829		
Diphyes dispar Chamisso and Eysenhardt 1821		
Diphyes chamissonis Huxley 1859		
Eudoxoides spiralis Bigelow 1911	Fish larvae; Copepoda	Alvariño (unpublished data)

PREDATION BY CTENOPHORA

Ctenophora are beautiful delicate marine animals commonly named comb-jellies, comb-bearers or sea walnutts. They have a gelatinous crystal clear or translucent appearance, of soft bluish or pinkish tonality with iridescent shine. They are generally spherical, ovoidal, or pearshaped organisms, except for the band-like *Venus* girdle specimens.

Ctenophora propel themselves through the water by beating strokes of their iridescent comb-like plates (comb rows or ribs), while the tentacles, in tentaculate species, are smoothyl trailed. These tentacles are retractile and are enclosed in the tentacle sheath or pocket at each side of the body. The tentacles are covered with filamentous lateral branches, which contain pinna with colloblasts or glue cells which secret an adhesive matter (Gudger 1943). These tentacles, when extended may stretch out to 20 cm or more.

Small crustaceans, young fish and other prey are continously caught on the adhesive cells of the tentacles, which contract and protrude actively during prey capture. The prey usually - dies immediately after touched by these cells, possibly due to a poisonous substance (Hyman 1940; Ralph and Kaberry 1950); a toxin extracted from the Ctenophora was observed to kill "small invertebrates and when injected into frogs, rabbits, toads and dogs elicits excesive skin secretion, muscular weakness, paralysis and death" (Hyman 1940). However, Lebour (1922) watched a *Pleurobrachia* attack and entangle a pipe-fish, which struggle for half an hour until succeeding in getting free, and no detection of any poisoning effect was observed.

The general accounts on the Ctenophora feeding behavior (Hardy 1956) indicates that they devour fish larvae, small crustaceans and other zooplankters (see Table III). They are considered by Bigelow (1926) to be of importance in the "natural economy of the plankton community". He reports that they are at times extremely abundant in the Gulf of Maine, and that - "they are among the most voracious of pelagic animals". Wherever Ctenophores swarm practically vacuum clean the waters and hardly any zooplankter can coexist with them. Ctenophores, excluding probably *Beroë*, can seriously affect the fisheries by predation on the planktonic stages of the animals of commercial importance, and all of them, including *Beroë*, are competitors for food with the meroplanktonic animals of commercial importance. More details of Ctenophora feeding behavior are given in

Harbison et al (1978).

Ctenophores occur some times in great numbers and may then seriously reduce the population of zooplankters upon which they prey, including fish eggs and larvae, crustacean and other zooplankters on which the fish depend for food. Bal and Prodham (1952) studies on the zooplankton of Bombay indicated that high number of Ctenophora coincided with a minimum number of fish larvae and young fish in that region. A peak of fish larvae occurred off Plymouth, England in the first fortnight of May 1930, but a low number of young fish, excluding Clupeidae, was found in the second fortnight of the same month (Russell 1930 a, b, 1935 a, b,). This coincided with high concentrations of medusae, siphonophores, and the Ctenophora *Pleurobrachia pileus*. During June, July, August and September of the same year, the numbers of Medusae, Siphonophorae and Ctenophora were high, - while the concentrations of fish larvae remained unusually low. The fish larvae catches for 1929 (Russell 1935a) were well below the average for the years 1930 to 1934, and during the hatching time in 1929 were present great quantities of ctenophores *Beroë cucumis*, *Belinopsis infundibulum*, *Pleurobrachia pileus*, and the Agalmidae siphonophore *Stephanomia bijuga* Russell's data indicate that the exceptional abundance of predator populations was responsible for the absence of the peak abundance of fish larvae normally occurring in the area.

Studies on plankton and herring in the Barents Sea (Mantenfel 1941) indicate that ctenophores feed actively on plankton which undoubtedly affects the survival and growth of the herring of the region. Swarming Ctenophora observed at the herring hatching grounds off Yorkshire, England, are discussed by Hardy (1956). "At such times these ctenophores must levy a very heavy toll upon young herring, and variations in their numbers from year to year must play a part in determining whether some broods of herring are more successful than other. It is possible that this may be one of the factors leading to the - well known fluctuations in the relative strength of different age-groups in a herring population".

Bigelow (1926) stated; "There is reason to believe that *Pleurobrachia* is a serious enemy of the successful reproduction of sundry fishes (e.g. cod and haddock) by feeding on their - buoyant eggs, few of which can escape destruction in localities where ctenophores are numerous". Mayer (1912) stated that "In cold northern waters where Ctenophora occur in vaste swarms, they constitute a serious menace to the cod fisheries by devouring pelagic eggs and young fish". Lebour (1922, 1923, 1925) - analyzed the food of ctenophores and found they feed on practical every type of plankton, including fish, and observed up to several fish per ctenophora stomach.

Plankton studies in the Gulf of Aden (Ali Khan and Hempel 1974) showed fish larvae in the digestive tract of Ctenophorae. In addition, Bigelow (1926) considered ctenophores to be serious enemies of gadoids and flat fish hatching at nursery - areas of the German Bank and the Banks of the North Atlantic extending to the Southwest of Cape Sable.

Russell (1931) in discussing the part played by crustaceans in the economy of the seas, stated that "the inmense swarms of plankton predators specially the Ctenophores, must play havoc among the copepod population and serve as serious competitors to the fish themselves, at times even depleting the supply. This is specially noticeable at times when ctenophores predominate in the catches, as on such occasions the remaining animal plankton appears exceptionally poor". Copepods in particular are exterminated in the centers of abundance of *Pleurobrachia*, though in their own turn they may swarm nearby; and it is common to find ctenophores packed with copepods or euphausiids and larval fish ingested and partially digested (Bigelow 1926). Bishop (1968) observed that Ctenophora feed selectively on Copepoda, eating *Pseudocalanus minutus* at greater rate than *Epilabidocera amphitritis* Ctenophores also have serious effects on the survival of shellfish larvae and spat production of oysters. *Pleurobrachia* is considered a serious - enemy of the oyster in Washington, due to the large amounts of larvae consumed by this ctenophore (Kincaid 1915), Nelson (1925) indicated that the abundance of the ctenophore *Mnemyopsis leidyi* appeared inversely related to the abundance of *Teredo*, *Bankia*, and the setting of *Ostrea* during 1921 to 1923 in Barnegat Bay and adjacent waters; the abundance of oysters setting in this region, Mulloca River and nearby regions correlated with the absence or scarcity of *M. leidyi*.

Feeding mechanism differ among the Ctenophora. The Tentaculata, represented by *Pleurobrachia*, spread their tentacles and feed on everything available in the waters. The Nuda Ctenophora, represented by *Beroë*, however, feed by engulfing and swalling food items by rapid suction, preying on larger organisms than the Tentaculata, which include also species of Tentaculata Ctenophora, thus limiting their populations.

Pleurobrachia is an inhabitant of the uppermost layers of the ocean, being found mainly along the upper 30-0m or 50-0m strata (Bigelow 1926). It is a voracious feeder; Lebour (1923) observed one 4mm-long *P. pileus* catch and partially digest a 10 mm-long *Gobius ruthenparry*. Fraser (1970) indicates that crustaceans are the dominant food, making up 80-97% of the total. The maximum amount found in a 13 mm-long *Pleurobrachia* included 1 *Calanus*, 1 *Centropages*, 44 *Acartia*, 4 *Evadne*, 2 *Podon* and 1 cyprid larvae of *Balanus*. Differences in the food found in *Plaurobrachia* stomachs will reflect the composition of the plankton of the area rather than differences in the selective diet of the Ctenophora. Kuhl (1932) described *Pleurobrachia* catching food in the aquarium: "The most usual prey-catching attitude is a stationary position with mouth upwards and the tentacles up to 20 cm long, with their lateral filaments extended like nets". Their hunting activity are displays of swimming in spirals "loop-the loop" turns, covering large spaces through the waters.

Studies on the distribution of *Clupea pallasi* larvae in British Columbia, Canada, from 1947 to 1952 (Stevenson 1962) describe predation caused by *Pleurobrachia* sp., together with numerous medusae and chaetognaths (with no determination of the respective species), indicating that "45% of the larvae in the sample had been or were being devoured by the Ctenophores". These ctenophores were so numerous in Mayne Bay that during - both day and night they appeared to form a false thick bottom at about 4 m depth, where they were observed preying heavily on fish larvae.

Large concentrations of *Pleurobrachia* at the northern part of Moray Firth, Scotland, concurred with absence of herring larvae, abundant at the adjacent regions where ctenophores were not present (Fraser, 1970). Swarms of *Pleurobrachia pileus* may be responsible of larval fish mortality, even if the larvae are not eaten by the ctenophores, which by consuming the food could affect the survival of the larvae, the adult herring and other plankton feeding animals of commercial importance Fraser (1970) explained that 1965 was a peak year for *P. pileus* in Scottish waters, when more than 47,000 were obtained in the northern North Sea; 6, 162 of these were examined for food content. The monthly average of those with food ranged from 4 to 60% with an annual average of 26%. During 1966, the monthly average resulted 4 to 40%, with 21.5% of yearly average, in 1967 the amount of ctenophores with food ranged from 0 to 58% and 19%, respectively, for monthly and annual average; during 1968 the feeding animals ranged from 0 to 10% monthly, and 27% for the year.

Bigelow and Leslie (1930) indicated that the plankton off Monterey (California) in 1928 presented high number of Copepoda and other planktonic organisms in various stations, but that "without exception they were relatively scarce wherever *Pleurobrachia* were plentiful". Kincaid (1915) indicated that the species feeds on Oyter larvae, and Lebour (1922) reported it eats *Calanus*, *Porcellana* larvae, and Chaetognatha.

The feeding behavior of other Cyppidae Ctenophora has been noted. *Mertensia ovum* has been observed by Bigelow (1909) entirely engulfing "a young sculpin (*Acanthias groelandicus* Fabricius) no less than 21 mm long, the victim being doubled up so to fit into the digestive cavity of the captor". *Hormiphora palmata*, a 40 mm long ctenophore with tentacles reaching 200 mm long when fully extended, excrets mucus which expands in a spider net pattern; it has been seen to catch and wrap specimens of the medusa *Sarsia* in this manner (Fukuchi, Yoshida and Hara 1971).

The Non-Tentaculata *Beroë* sp. are large and more voracious than the other ctenophores (Bigelow 1926). Lebour (1922) stated that when *Beroë* and *Pleurobrachia* are present together, the former feeds on the latter. *Beroë* has a rapid digestive activity devouring *Pleurobrachia* and *Bolinopsis* (Bigelow 1926), and it always less abundant than either of the latter, which reflects on the equilibrium found in their respective populations.

Studies on the sensorial mechanisms of *Beroë cucumis* and *B. ovata* by Horridge (1965b) showed that juice of pulverized *Pleurobrachia* applied to the lips of *Beroë* caused a strong feeding response, and when *C. cucumis*, *B. ovata*, and *Pleurobrachia* co-occur, the long tentacles of *Pleurobrachia* are caught by the current at the side of *Beroë* which rapidly engulf and swallow the *Pleurobrachia*.

Beroë could accidentally digest crustaceans or fish, but when remnants of those organisms are found in *Beroë* may come from the food in the prey consumed by the ctenophores (Kamshilov 1960b). Mantenfel (1941 considered that *Beroë* probably fed on herring in the Barents Sea. Kamshilov (1960 a,b), indicated that a 35 mm-long *Beroë* swallowed and digested 31 *Bolinopsis* about 20 mm-long, and that it also fed on *Pleurobrachia*. However, Phillips et al (1969) described *Peprilus alepidotus* (harvest fish) as commensal with *Beroe ovata*, and Matthews and

Shoemaker (1952) observed the fish *Palinurichthy* sp., *Syngnathus*, *Hemicaranx amblyrhynchus*, and *Chloroscombrus* (*Scomber*) *chrysurus*, swimming in and out of *Beroe* in the Mississippi Sound near Biloxi, Mississippi.

Beroë usually inhabit the deeper layers, to about 100 m - depth, avoiding the surface waters where there is danger of the "destructive wave action" (Bigelow 1926).

The swimming activity increases in both *Beroë* and *Bolinopsis* in the presence of the prey (Swanberg 1974) or the swarms of prey animals.

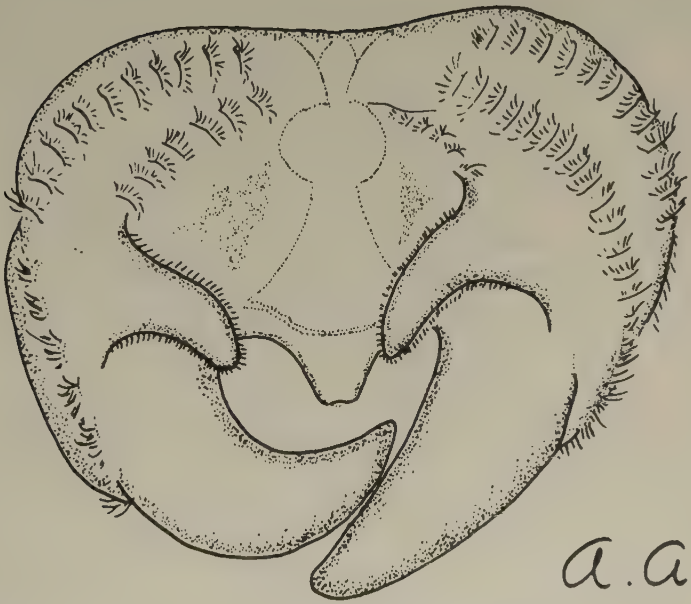
Bolinopsis infundibulum move through the water with "their large paired peristomieae (oral) lobes expanded like trawl-doors, and these were observed came together occasionally to enclose quantities of water containing food organisms (Nagabushanam - 1959). *Bolinopsis* are extremely voracious, and calculations by Kamshilov (1960b) indicated that 2 *Bolinopsis* can eliminate in one month a population of *Calanus* at a concentration of 300 per m^3. A 23 mm-long *B. infundibulum* was observed to capture 18 small copepods of various species and 15 cladocerans, all of which was digested in 58 minutes; 2.5-3 mm specimens digested one *Calanus* per hour and 10 to 11 in two hours. They will also take capelin larvae although it will take several hours to digest (Kamshilov 1960b, Kamshilov et al 1958).

Bolinopsis infundibulum appeared in the plunger jars and aquarium tanks at Plymouth (Lebour 1922, 1925) containing *Lophius piscatorius* (anglers) larvae, together with copepods, on which the larvae had been actively feeding; but although it was thought that *B. infundibulum* would prey on copepods and the anglers larvae would be safe, this was not the case. *B. infundibulum* caught and devoured the fish larvae. Lebour (1925) described 4 to 30 mm *B. infundibulum* grabbing the larvae with - their tentacles. Although the fish struggled, the lobes of the ctenophore would close on the prey, engulfing it within its mouth; it was then conveyed to the stomach to be promptly digested.

Predatory behavior has also been described for the ctenophores *Leucothea multicornis* and *Mnemyopsis* sp. The activity of the pulsations of the oral lobes and tentacles of *L. multicornis* were observed to increase with the presence of prey organisms (Horridge 1965a). The gathering of bunches of plankton performed by this species were typical (carying them to the mouth). Plankton animals were not attached to the finger-like protrusions scattered over the body of the ctenophore but only on the tentacles and oral lobes. The fingers dart out and - strike the passing zooplankton, which immediately become partially paralyzed. It appears that some powerful poison is present at the tip of the fingers, probably produced by the large glandular cell. The fingers (Horridge 1965a) are extremely sensitive to vibrations, and a 100 µm at 10 c/s vibration 5 mm - away from the tip of the finger is detected. A disturbance of this degree may be produced by a copepod or other zooplankter, with the finger extending about 5 mm to reach the prey.

The feeding mechanism of *Mnemyopsis leidyi* was described by Main (1928). Nelson (1925) observed these animals in Barnegat Bay during several years and seasons and found that at summer temperature (more than 20°C), the rate of digestion of food and ejection of residues are so rapid that it is necessary to examine the specimens just at the time of capture, as the stomoderm empties in 20 to 30 minutes. *M. leidyi* 5 to 70 mm in polar length from Solomon, Maryland, were observed to feed on *Acartia tonsa*, consuming 472 copepods per hour, but the rate of feeding changedin relation with the concentration of copepods and the size of the ctenophore, the large specimens consuming more food (Bishop 1967). However, *M. leidyi*, the most abundant zooplankter in the estuaries of the mid-Atlantic United States, itself experiences a reduction in its biomass in spring with the occurrence of the Medusae *Chrysaora quinquecirrha* and the Nuda ctenophore *Beroë ovata* which feed actively on *M. leidyi* (Miller 1974). *M. mccradyi* appears to be one of the most important bioeconomic plankton species in the Mississippi Sound, inhabiting the surface waters in concentrations of 10-100 individuals per m^2, and feeds on microplankton, resulting in a drastic reduction on the zooplankton abundance with the increase in numbers of *M. mccradyi* (Phillips et al 1969).

Reported accounts and observations on the food of ctenophores show that they are carnivores and may produce serious devastation of zooplankters. However, Ctenophora appear in patchy distribution and are mainly abundant in close to shore waters where productivity is usually extremely high, because of the occurrence of larvae of benthic and coastal Crustacea, Mollusca, Annelids, etc. Ctenophora may, in this context, act as a regulatory agent of those populations, while other zooplankton populations survive in the more offshore locations, away from the activity of dense populations of ctenophores. However, the Cte nophora populations themselves may be limited by predation of some species of Ctenophora on other species of the same group.



CTENOPHORA: *Ocyropsis maculata* **(Rang) 1828**

TABLE III. OBSERVATIONS ON THE FOOD OF CTENOPHORA

Order: Family Species	Food	Author
CYDIPPIDAE: Mertensiidae		
Mertensia ovum (Fabricius) 1780	*Acanthias groenladicus* (young Sculpin fish), and other zooplankters	Bigelow, 1909
	Fish larvae	Mayer, 1912
Lampea pancerina (Chun) 1880	Salps (Tunicata)	Harbison et al. 1978
: Pleurobrachiidae		
Pleurobrachia sp.	Oyster larvae	Kincaid, 1915
	Calanus (Copepoda); *Porcellana* larvae and other Crustacea; Chaetognatha	Lebour, 1922
	Shellfish and other Mollusca larvae	Nelson, 1925
	Eggs and fish larvae; Copepoda; Euphausiidae; small Crustacea; Coelenterata; Chaetognatha	Bigelow, 1926
	Copepoda	Bigelow and Leslie, 1930
	Young fish	Hardy, 1956
	Capelin larvae; *Calanus* (Copepoda); Euphausiidae; other Crustacea; other Ctenophora	Kamshilov, 1959
	Eggs and larvae of cod, Mackerel, haddock and other fish; Copepoda; Euphausiidae; Decapoda larvae; Chaetognatha	Fraser, 1962
	Clupea pallasi larvae	Stevenson, 1962
Pleurobrachia bachei L. Agassiz 1860	*Pseudocalanus minutus* copepodites and adults (Copepoda); nauplii larvae	Bishop, 1968
	Labidocera trispinosa, *Acartia tonsa*, *Calanus helgolandicus*, *Corycaeus* (Copepoda); *Artemia salina*; Cladocera; Chaetognatha; other zooplankters	Hirota, 1972
	Labidocera trispinosa, *Corycaeus anglicus*, *Oncaea*, *Paracalanus parvus*, *Euterpina acutifrons*, *Acartia tonsa*, *Rhincalanus nasutus*, Copepod eggs and nauplii; *Evadne nordmanni*, *E. spinifera* (Cladocera)	Hirota, 1974
Pleurobrachia globosa Moser 1903	Fish eggs and larvae; Copepoda; Chaetognatha	Nagabhushanam and Jothinayagam, 1977
Pleurobrachia pileus (Fabricius) 1780	Any planktonic organism	Bigelow, 1915

TABLE III. Cont.

Order: Family Species	Food	Author
	Labrus and other fish larvae; *Calanus finmarchicus*, *Centropages typicus* (Copepoda); *Porcellana* and *Gebia* larvae, crab zoea and other Crustacea larvae; Chaetognatha	Lebour, 1922
	Young *Cottus* and *Labrus*, *Syngnatus* (pipe-fish), *Gobius rutherparry*, plaice eggs and herring larvae; *Calanus*, *Temora*, *Pseudocalanus* (Copepoda); *Gebia* and other Crustacea larvae; Euphausiidae; Mysidacea; Cumacea; Chaetognatha; *Oikopleura* (Appendicularia); other Ctenophora	Leobour, 1923
	Fish larvae; Copepoda; Chaetognatha	Alvariño, 1956a 1956b
Pleurobrachia pileus (Fabricius) 1780	*Oithona nana*, *O.similis*, *Acartia clausi*, *Paracalanus parvus*, *Pseudocalanus elongatus*, *Calanus helgolandicus*, *Centropages Kroyeri*, (Copepoda), *Evadne spinifera*, *E. tergestina*, *Podon* (Cladocera); Crustacea larvae; Lamellibranch larvae; Polychaeta; Chaetognatha; *Oikopleura dioica* (Appendicularia)	Lazareva, 1962
	Eggs and fish larvae; eggs, nauplii and adult *Calanus* and other Copepoda; Euphausiidae; Amphipoda; Mysidacea; *Evadne*, *Podon* (Cladocera); Cumacea; Decapoda and Cirripedia larvae; Lamellibranch and Echinodermata larvae; *Oikopleura*, *Thaliacea* (Tunicata); Phytoplankton	Fraser, 1970
	Calanus plumchrus (Copepoda)	Lee, 1974
Hermiphora palmata Chun 1898	*Sarsia* (Medusae)	Fukuchi, Yoshida and Hara, 1971
Lampetia (Hormiphora) sp.	Salps (Tunicata)	Hamner et al, 1975
LOBATA: Bolinidae		
Bolinopsis sp.	Clupeidae, other fish larvae, and other zooplankters	Mantenfel, 1941
	Copepoda	Fraser, 1962
Bolinopsis infundibulum (O.F. Müller) 1776	Microplankton	Lebour, 1923
	Lophius piscatorius and other fish larvae	Lebour, 1925
	Various zooplankters	Alvariño, 1956a
	Pseudocalanus elongatus, *Acartia clausi*, *Temora longicornis* (Copepoda) *Evadne nordmanni*, *Podon intermedius* (Cladocera); nauplii larvae	Nagabushnam, 1959
Bolinopsis infundibulum (O.F. Müller) 1776	*Gadus capellanus* larvae,	

TABLE III. Cont.

Order: Family Species	Food	Author
	Calanus (Copepoda)	Kamshilov, 1960b; Kamshilov et al, 1958
	Pseudocalanus elongatus, *Centropages hamatus*, *Temora longicornis*, *Oithona similis*, *Oncaea borealis*, *Microsetella norvegica*, *Acartia longiremis* (Copepoda); *Evadne nordmanni*, *Podon leuckarti* (Cladocera); Cirripedia nauplii; *Synchaeta* (Rotatoria); *Tintinopsis*, *Campanula*, *Helicostomella subulata* (Tintinnoidea)	Loginova and Perzov 1967
Bolinopsis vitrea L. Agassiz 1882	Copepoda; Ostracoda	Swanberg, 1974
Leucothea multicornis Fewkes 1882	Various zooplankters	Horridge, 1965a
Mnemyopsis leidyi A. Agassiz 1865	Copepoda; *Oyster* and other Mollusca larvae (*Teredo*, *Bankia*); detritus	Nelson, 1925
	Acartia Tonsa (Copepoda)	Bishop, 1967
	Entomostracea	Miller, 1974
	Fish eggs and larvae; Copepoda; Cladocera; Mysidacea; Amphipoda; Cumacea; Brachyuran and Cirripedia larvae; Annelida; Mollusca	Burrell and van Engel, 1976
	Acartia tonsa (Copepoda)	Kremer, 1979
Mnemyopsis mccradyi Mayer 1900	Microplankton	Phillips et al, 1969
	Copepoda; *Barnacle* nauplii; Mollusca Veliger larvae	Baker and Reeve, 1974
Eurhamphaea vexilligera Gegenbaur 1856	Copepoda	Harbison et al, 1978
Ocyropsis chrystallina Rang 1828 *O. maculata* (Lesson) 1843	Small fish; Copepoda; *Hyperid* Amphipoda; Euphausiidae; Beroë	Harbison et al, 1978
CESTIDA		
Cestus veneris Lésueur 1813	Copepoda	Harbison et al, 1978
BEROIDA: Beroidae		
Beroë sp.	Other Ctenophora, and zooplankters	Chun, 1880
	Pleurobrachia, *Bolinopsis*	Bigelow, 1926; Kamshilov, 1960a

TABLE III. Cont.

Order: Family Species	Food	Author
	Herring larvae and juveniles; other zooplankters	Mantenfel, 1941
Beroë cucumis Fabricius 1780	*Pleurobrachia*	Mayer, 1912
	Calanus finmarchicus, *Centropages typicus*, *Pseudocalanus elongatus* (Copepoda); *Podon intermedius* (Cladocera), other Crustacea; *Pleurobrachia pileus*	Lebour, 1922
	Calanus (Copepoda); other crustacea; *Pleurobrachia*, *Bolina*; *Coscinodiscus* (Diatomacea)	Lebour, 1923
	Pleurobrachia	Horridge, 1965b
	Bolinopsis vitrea, *Eurhamphaea vexilligera*, *Ocyropsis maculata*, and other zooplankters	Swanberg, 1974
Beroë ovata Chamisso and Eysenhardt, 1821	*Pleurobrachia*	Horridge, 1965b
	mnemyopsis leidyi	Miller, 1974; Burrell and van Engel, 1976
	Bolinopsis vitrea, *Cestus veneris*, *Ocyropsis chrystallina*, *O. maculata*, *Leucothea multicornis*	Swanberg, 1974

PREDATION BY CHAETOGNATHA

Plankton indicator species such as Chaetognatha are useful in fisheries research to identify the characteristics of rich or poor water regions, which in turn affect fish populations (Russell 1939). Plankton conditions may thus operate in two ways; influencing the survival of recently hatched fish producing a strong parental population and causing the alteration of the routes of migration of fish.

Such an example is the rich plankton *Sagitta elegans* waters and poor plankton content of the *S. setosa* waters, a well-documented fact in the work of many years by Russell and others at the Marine Laboratory in Plymouth, England; similar studies have been carried out in Scotland by Fraser (1952, 1961). Rusell (1939) noted that the highest percentage of *S. setosa* occurring in 1938 coincided with the lowest amount of spring fish larvae (Clupeidae not included). However, the lack of data on the fish larvae for other seasons, and the exclusion of the Clupeidae larvae, may in some cases, alter the results to some degree.

Chaetognatha feed on Copepoda, other Chaetognatha, Ostracoda, Medusae, Salps and the larvae of other marine animals (Oye 1918). The food of the chaetognaths is concidered heterogenous (Della Croce 1963), including cannibalism, and representants of every group in the plankton: diatoms, ciliates, Tintinnids (Protozoa, Medusae (Coelenterates), Crustacea, Copepoda, Amphipoda, Cladocera, larval stages of Crustacea, Mollusca Pteropoda and Heteropoda, Chaetognatha, Tunicata, fish eggs and larvae. A listing of food of chaetognaths is given in Table IV.

Analysis of the intestinal content of Chaetognatha from the Northeast of Amazon estuary included cuticle of copepods and fragments of Dinoflagellates, diatoms and radiolarians (Barth 1963). Rakusa-Suszczewski (1969) indicated that in summer *S. elegans* from the North Sea was feeding on *Pseudocalanus elongatus* and *Calanus finmarchicus* showing a preference for the former, even when *C. finmarchicus* was the most abundant species in the region. The selection by *S. elegans* of *P. elongatus* contributed to the decrease of this species in the waters and to the greater relative abundance of *C. finmarchicus*. Analyses of food content of few individuals of *S. elegans* from the Baltic Sea (Rozanska 1971) indicated 2 to 12% with food in their guts, and an increase of intake of food during daylight, while feeding mainly on copepods. Studies of the Chaetognatha population of Southeastern Australia (Thomson 1947) show that they feed mainly on Copepoda, fish larvae and other chaetognaths, and are considered to play an important part in the food cycle of the pelagic communities because of their role as competitors and prey. Chaetognatha eat larvae of fish and of small crustacea (Johnson and Snook 1927), young fish (Graham et al 1954); fish larvae, copepods ciliates and cannibalism was more outstanding in *Sagitta enflata*, *S. hexaptera* and *S. hispida* (Suarez-Caabro 1955 and author's data); preying also on fish larvae, copepods, euphausiids, cladocerans, amphipods other crustacea and the larvae of other animals of commercial importance (Alvariño 1962, 1965, 1974). The prey in the digestive tract of chaetognaths from the Agulhas Current region (Stone 1969), *S. enflata*, *P. draco*, *S. bipunctata*, *S. serratodentata*, *S. hexaptera*, *S. robusta*, *S. lyra*, *S. friderici*, *S. ferox*, *S. minima*, *S. regularis*, *S. decipiens*, *S. bedoti*, *K. subtilis*, *S. planctonis*, included Copepoda and other Chaetognatha, and were not found eating fish larvae, in a region where Clupeidae and *Merluccius* fish populations are abundant. In the Agulhas Current region it is expected that the large specimens of Chaetognatha would be devouring a good amount of fish larvae.

The food organisms found in the digestive tract of chaetognaths from the Hilutangan Channel, Philippines, in January 1972 (Jumao-as and Westernhagen 1975) included 401 Copepoda (74.8%), 105 Chaetognatha (19.6%), 7 Foraminifera (1.3%), 6 Echinoid larvae (1.1%), 6 Decapod larvae (1.1%), 4 fish larvae (0.8%), 3 Tunicata (0.6%), 1 Polychaeta larvae (0.2%), 1 Isopoda (0.2%) and 1 veliger larvae (0.2%). The species observed were *S. enflata* (the most abundant and showing highest degree of cannibalism), *S. neglecta*, *S. robusta*, *S. regularis*, *Krohnitta pacifica*, *S. bedoti*, *S. decipiens*, *S. pulchra*, *S. ferox*, *K. subtilis*, *S. pacifica* (as *S. serratodentata*), *P. draco*, *S. hexaptera*. Jumao-as and Westernhagen (1975) did not find considerable variations in dietary composition with season and standing crop of the plankton communities.

The stomach content of the Chaetognatha collected in the Arabian Sea during the International Indian Ocean Expedition (Nair and Rao 1973) included fish larvae, Polychaeta larvae, Ostracoda, other chaetognaths, Copepoda (*Centropages*, *Eucalanus*, *Corycaeus*, *Cithona*, *Lucicutia*, *Oncaea*) and rarely *Harpacticoid* copepods.

Several authors have given accounts of their observations on the effects of chaetognath populations on fish larvae. The consistent presence of fish larvae in the gut of Chaetognatha (Lebour 1922, 1923) indicates these animals prey on young fish, mainly *Clupea harengus*, in the North Atlantic. Similar situations (Bigelow 1926) show that chaetognaths should be a serious menace to the stock of various fish in the Gulf of Maine region. Corbin (1947) published data on *Scomber scombrus* and *Sardina pilchardus* larvae, together with information on co-occurring abundance of Chaetognatha *S. setosa*, *S. elegans*, *S. tasmanica* (as *S. serratodentata*), *S. lyra* and the Siphonophore *Muggiaea atlantica*. The data show that, the presence of *S. scombrus* larvae coincided with no or few Chaetognatha or Siphonophorae, and high concentrations of these chaetognaths occurred with few or absence of *S. scombrus*. Similar observations were made for chaetognaths off California (Alvariño 1979, 1980b) primarily between *S. enflata*, *S. hexaptera* and *S. scrippsae*, and *Engraulis mordax* larvae.

Zooplankton studies off Bombay during 1944 to 1947 (Bal and Pradham 1952) indicated that highest number of *Sagitta* coincided with lowest amount of fish larvae. In 1945 the high number of chaetognaths did not correspond to a low number of fish larvae; however, a high concentration of copepods occurred, which may have affected the results, as was also demonstrated in Alvariño (1980b). The quantitative distribution of chaetognaths (Furnestin 1960) *S. setosa*, *S. enflata*, *S. serratodentata*, *S. bipunctata*, and *Engraulis encrasicholus* larvae, indicated that highest concentrations of chaetognaths coincided with low numbers of anchovy larvae and vice-versa. Studies on the distribution of Chaetognatha at Coringa Bay, India (Rao 1962) also include data on plankton; and when Chaetognatha, Ctenophora (*Pleurobrachia*) and Medusae were abundant, no or few fish larvae were observed, and vice-versa.

Ecological survey studies of the Scottish fishery and the changes in the plankton during the period 1949 to 1959 (Williams 1961) include data on Copepoda, Chaetognatha, Euphausiidae, young fish and eggs obtained with the Hardy Plankton Recorder; although the data are presented in annual averages, it can be found that in more than 50% of the yearly periods, high concentrations of large chaetognaths coincided with low averages of fish larvae. Plankton collections obtained at Eddystone, off England during several months of 1958, 1959, 1960 showed (Southward 1962) that highest concentration of *S. elegans* and *S. setosa* coincided with no Clupeidae larvae, and highest number of these larvae or any other fish occurred with scattered specimens of *S. setosa* and/or *S. elegans*, and high concentrations of the medusae *Liriope tetraphylla* and the siphonophore *Muggiaea atlantica* and moderate amount of chaetognaths, coincided with no fish larvae.

The distributional characteristics of the plankton in the oceanic fishing grounds of salmon in the North Pacific (Tsuruta 1963) showed in 80% of cases that, high concentration of *S. elegans* or medusae concurred with absence of Pleuronectidae and Gadidae fish larvae. In the tuna fishing grounds of the Marshall, Gilbert and Phoenix Islands, the abundance of *S. bipunctata* coincided with scarcity or absence of fish; and in waters around Bikini Atoll, high concentration of any of the chaetognaths (mainly *S. pacifica, S. hexaptera, S. enflata, Pterosagitta draco*) coincided with lowest occurrence of fish larvae. In the tuna fishing grounds of the Indian Ocean, off Nias Islands, concentrations of any of *S. bipunctata, S. pacifica, S. enflata, S. regularis* species coincided also with scarcity or absence of fish larvae (Tsuruta 1963).

Systematic list of zooplankters (Lakkis 1971) at surface waters off Lebanon during 1969 show, that lowest quantities of fish larvae coincided with large amounts of Medusae, Chaetognatha, and Ctenophora, and highest concentrations of fish larvae and eggs with high numbers of Copepoda and Cladocera.

Observations on the feeding of *S. elegans* from the northwest North Sea (Wimpenny 1937) indicate they eat Copepoda, mainly *Calanus finmarchicus*. The number of individuals containing food was greatest in June and July, with an average of 30.5% for the whole year. Analyses of the diagrams from Wimpenny (1937) for *S. elegans, S. setosa, C. finmarchicus*, show that for 1934, high concentrations of *C. finmarchicus* coincided with no *S. elegans* and *S. setosa*, and vice-versa, and that the distribution of the copepods agreed with concentrations of phytoplankton they were feeding on; thus an inverse relation was found for the proportion of food in the stomachs of chaetognaths and the density of the zooplankton populations, which appeared more abundant in regions rich in phytoplankton, where copepods will be grazing. Studies of zooplankton in the northwest north Sea (Bainbridge and Forsyth 1972) correlat the relation of zooplankton with physical changes in the environment and in the herring stock in an attempt to understand the dramatic changes observed in this fishery, which diminished progressively until its virtual disappearance. The study of the plankton showed the presence of lar ge quantities of *Sagitta* (no specific data) and *Tomopteris*, with a positive relation with the total number of Copepoda, principal food of herring. Thus the fluctuations in the abundance of *Calanus* and *Spiratella* (main food organisms of herring) and abundance of plankton predators could have caused the numbers of fish larvae to decrease drastically.

In St. Margaret's Bay, Canada, the *Sagitta elegans* biomass was found to be negatively related (Sameoto 1975) with zooplankton biomass (*Pseudocalanus*, *Temora*), while the Cladocerans *Podon* and *Evadne* and the copepod *Eurytemora* were positively correlated to either *S. elegans* number or biomass. It was implied that the animals may be reacting to one another or to environmental factors to which they respond positively or negatively, although the negative correlations observed may have been produced by a predatory/prey activity.

Mechanical waves contitute the most efficient transmission in the waters, and the vibrations produced by prey, enemies, etc., are registered by the aquatic animals. Water vibrations elicit an escape reaction, unless the vibrations are of the frequency range and amplitude adequate for the animals to make an accurate movement towards the prey to catch it. The nervous system of the chaetognaths includes some mechanisms of integration which discriminate the characteristics signal of the typical prey, its distance and dart direction (Horridge and Boulton 1967). The eyes of the chaetognaths are of a particular structure with at least five lenses pointing in different directions.

The animals are transparent, and they can see down through their own body (Hardy 1956). Eakin and Westfall (1964) indicated that since Chaetognatha inhabit the subsurface oceanic waters where light is weak and diffuse, the small lenticular bodies within the eye might be useful for a sufficient perception of the light to stimulate the photoreceptor tubules; they even tempt to speculate that the conical body in the photoreceptors cell might have wave guide effects or that it might act as a resonator in the manner of a laser. The accuracy of vision in Chaetognatha is unknown in regard to determination of the location and distance of the prey, and because of their indiscriminating feeding at daylight and night, it is assumed that they might detect the victim by a vibration sense, located in the ciliar tuffs and bristtles scattered over their body, and the corona ciliata which may function also as chemoreceptor.

Because Chaetognatha feed both in the dark and in light, it may be that capture of prey is unaffected by the presence or absence of light, suggesting that they may have another mechanism besides the visual detection, such is the perception of the prey by vibrations produced or chemicals released (Scheuer 1977). *Spadella cephaloptera* (benthic chaetognath) fed well in daytime, and *Sagitta* species dart directly towards a moving prey in the light, rather than relying on chance contact for food (Reeve 1964). *Spadella cephaloptera* under laboratory conditions was able to make accurate feeding movement towards any source of vibrations are 9 to 20 c/s with an amplitude of 100 to 500 μm at the distance of 1 to 3 mm (Horridge and Boulton 1967). It was then observed that *S. cephaloptera* attacks only with a small range frequency (9 to 20 c/s), and that is also sensitive to the amplitude of the vibration of 100 to 500 μm at a distance of 1 to 3mm. The responses fall off above 20 c/s or below 9 c/s for a vibration of constant amplitude.

Spadella were observed to grab the prey (Parry 1944) only when it is above or behind its head, which may indicate the tactile or other sensitivity receptor role of the corona ciliata. The food organisms appear in the gut of chaetognaths, with the heads toward the anus of the chaetognaths, which indicates Chaetognatha attack head on. Hardy (1956) explained the behavior of Chaetognatha in the ocean, resting motionless until a prey organism swimms by and suddenly at "lightning speed" the chaetognath dart forward, in the appropriate direction, propelled by the violent up and down flapping of the tail, striking with - speed and accuracy, capturing the prey with the rapid grab of the hooks and teeth. In this manner, chaetognaths are able to cover in a flash by their dart swimming 5 or 6 times their own length.

Experiments on *Spadella* showed that their actual feeding - response can be triggered by a source of vibration of approximate correct combinations of amplitude, frequency, and location. General vibration is ineffective (Horridge and Boulton 1967) because strong stimuli excessively close to the ciliary organs produce an escape movement response. This indicates the nervous system of chaetognaths must include some mechanism (Horridge and Boulton 1967) to identify the characteristic signals of a typical prey, its distance, and location. Chaetognatha probably use both their sensory mechanism, vibration and chemical sensitivity, and the eyes, to capture food. Their unimpaired feeding ability in the dark indicates that chaetognaths may well rely to a large extent on the numerous tangoreceptors covering their body and the corona ciliata, and under light conditions by using also the eyes perception. In this manner they alternate use of both methods of sensory perception to capture food, under dark and light conditions.

S. elegans and *S. setosa* were observed by Rakusa-Suszczewski (1969) feeding more actively at night (in agreement with Pearre 1973 for *S. elegans* from Bedford Basin, Nova Scotia), and a relation was found between the frequency of food species in the gut content of the predators and its frequency in the biotope, and large species were able to grab larger food individuals, being possible to obtain the size range of food depending on the size of the predators. However, continuous daily studies by Mironov (1960) on the food of *S. setosa* from the Bay of Sevastopol indicated that "apparently the intensity of feeding is not linked with any particular time of day", but rather is related to the availability of food.

To try to determine the daily food ration of *Sagitta*, Mironov (1960) assumed that the longer period of time necessary to digest food (Copepoda and other Crustacea), the more probable it is that individuals with full intestines will be found more frequently than individuals with empty intestines. Conversely, the shorter the digestive time (fish larvae prey), the more often are found individuals with empty digestive tracts. The fact that many chaetognaths are found with no food in the digestive tract indicates that may be a long period between evacuation of remains of previous meal and intake. No or few individual with empty intestines would be observed if feeding follows immediately evacuation of remains of previous meal. Availability of food, length of digestion time, and regurgitation of food by animals under the stress of capture are factors which must be considered.

Copepoda are more frequently found in the gut of chaetognaths due to a variety of factors; for example, need to capture more individuals of this group than fish larvae to fulfil the nutritional requirements; the exoskeleton of Copepoda lasts a far longer time under attack by the digestion process and remains longer in the digestive tract before expelled; and Copepoda constitute the most abundant zooplankters and are therefore always available.

In the digestive tract of Chaetognatha I observed fish larvae at advanced stages of development more often than yolk sac larvae. In fact, yolk sac larvae are very rarely seen in the stomachs of chaetognaths. Either the yolk sac larvae are rapiidly digested by the Chaetognatha reducing the chances to observe them, or Chaetognatha more efficiently detect the vibrations produced by the swimming of well developed larvae than those by the yolk sac larvae. The feeding behavior of Chaetognatha described by Newbury (1972) to catch food organisms appears closely related to the activity of the prey. *Sagitta - hispida* consumed actively swimming *Artemia* but not their eggs swirling in the waters, and also fed on living plankton while ignoring dead organisms. These observations indicate that chaetognaths locate and attack the prey when the latter is actively swimming, producing vibrations and turbulence in the waters. Such is, the vibration produced by the continuous filter-feeding Copepoda, which fit within the range of vibration to which Chaetognatha respond. Chaetognatha may select specific copepods by the frequency of the vibrations produced. There is an evident need for more experimental work on the vibration rate registered by each species of chaetognath under various environmental conditions, and the vibration ranges produced by the organisms considered food of Chaetognatha, to properly understand their feeding behavior and feeding pattern, and to elucidate the part played by sensorial organs in the feeding behavior.

Kotori (1969) estimated that the maximum consumption of food is always lower than the amount of existing food organisms (and it must be or they will starve), and that Chaetognatha may consume 8.1 to 70 % (average 23.5 %) of the standing crop of food organisms in the waters they inhabit. Mironov (1960) calculated that *S. setosa* consumed daily about 0.5 % of the mean available plankton biomass. These estimations will fluctuate drastically with the number of chaetognaths, species, the dominant stage of development, type of food, and condition of the populations.

Laboratory experiments show that *Sagitta hispida* has a maximum rate of ingestion (Reeve 1964) which will not exceed with the availability of food, and field observations by Nagasawa and Marumo (1972) on *S. nagae* indicated the food contained ratio was "affected neither by food density nor by the copepod number per *Sagitta*". Indeed, laboratory observations on the feeding behavior of chaetognaths indicate they are adapted to use and encounter concentrations of food organisms which are patchily rather than uniformly distributed and at low density (Reeve et al 1975).

Revee (1964) observed the feeding behavior of *S. hipida* during long periods (tropical Atlantic species) maintaining one specimen per each 50 ml jar in the laboratory. *Artemia* nauplii were offered as food to each jar to measure the feeding capabilities of *S. hispida*. It was found that they capture more than an average 2 *Artemia* per hour, but if starved will take several in a few minutes. Feeding rates increased with the size of the and selection of food increased with age. *S. hispida* ingested up to 64 %, and 37.6 % for *S. nagae* (Nagasawa and Marumo 1972) own dry weight of food per day, and herbivores in a natural community reached a maximum of only 30 % (Riley and Bumpus 1946).

One to two day-old *S. hispida* appeared to be able to recognize and deal with food as does the adult (Reeve and Walter 1972), feeding on copepod nauplii and copepodites of *Acartia tonsa* and *Oithona nana*. They did not take Rotifera or ciliates, perhaps due to their large size or because they did not produce the type of vibrations which stimulate the sensory apparatus of the chaetognath. The size of food ingested is related to the maximum expansion of the mouth of the chaetognath.

The food passed in 8 seconds to the end of the gut immediately following ingestion, and if several prey organisms are ingested in rapid succession, they are lined up, one in front of the other, occupying the whole length of the gut. In this manner it appears (Cosper and Reeve 1975) that an adult *S. hispida* could capture enough food at one time to satisfy its optimal nutritional requirements for a 24-hour period. Data on the duration of digestion in various Chaetognatha is presented in Table V.

Sagitta hispida can live without food for at least 7 days using body protein as energy source (Reeve 1964). Lee (1974) explained that the protein does not have an energy storage function and low levels of neutral lipids are associated with plankton with constant feeding requirements such as Chaetognatha, Ctenophora, both low in neutral lipids; thus species of those groups can starve within 48 hours if they do not eat.

Chaetognaths do not store food reserves and their high - need of proteins results in a high active predatory capacity. Data on digestive efficiency (Cosper and Reeve 1975) of these carnivores, for instance, *S. hispida*, suggest that a 400 μg dry weight adult ingests a maximum of about 9 % of its own weight in food per day, or 37 μg dry wight, feeding on copepods, and will be most efficient preying on fish larvae.

The estimations of Sameoto (1972) on the K-cal consumed by *S. elegans* was higher than the estimated Copepoda production for the period, therefore suggesting that *S. elegans* may have another source of food which was not recorded in the samples analyzed. The food was probably fish larvae, which is digested rapidly after ingestion and thus offer few chances to be observed in the gut of the chaetognaths collected.

Studies on feeding behavior of *S. elegans*, the only chaetognath taken in the waters near the southeast coast of Newfoundland (Fraser 1969) suggest that after sorting the collections in the laboratory within an hour after capture, most of individuals were dead and of those still alive, only 5% survived overnight; no feeding was observed in these dying plankters. At Plymouth I also observed the jars with alive plankton - brought daily to the laboratory. The species included, *S. elegans* and *S. setosa* could be seen darting about actively catching fish larvae and copepods; however, their activity diminished progressively with the physical deterioration of the body which apparently impaired the normal physiology of the animal, until they died. Similary I observed the same results with *S. euneritica* and *S.enflata* collected off Scripps Pier and off San Diego, California. The vacuolar collarette-like tissue covering totally the body appears to be affected, the animal cannot regenerate this tissue, the anatomical damage is not reversible, and the specimens endure a progressive deterioration until death. The best method to collect chaetognaths alive is with a bucket, in this manner they are caught together with a good amount of water, and the body of these animals is not mechanically damaged or suffers any other kind of injury.

In most cases, the above mentioned Chaetognatha were not in a normal, healthy condition when observed in the laboratory and the animals were growing progressively weaker and consequently their physiologic functions would not be performed at a proper rate. Further more, digestion of Crustacea would be more laborious than digestion of soft body zooplankters such as Chaetognatha or fish larvae, as the digestive activity necessary to break down the external teguments to reach the digestive parts of the body of the animals is greater for the crustaceans than for the soft body prey. This should be kept in mind when comparying laboratory results to the feeding and predation processes in the oceans, and when making assumptions about the impact of predation on fisheries.

TABLE IV. OBSERVATIONS ON THE FOOD OF CHAETOGNATHA

Species	Food	Author
Spadella cephaloptera Bush 1851	Copepoda	Parry, 1944
	Artemia	Horridge and Boulton, 1967
Spadella gaetanoi Alvariño 1978	Copepoda; Invertebrate larvae	Alvariño, 1978
Eukrohnia fowleri Ritter-Zahony 1909	Copepoda; Euphausiidae	Furnestin, 1959; Alvariño (unpublished data)
	Copepoda; Radiolaria	Tchindonova, 1959
	Calanus pacificus, *Lucicutia bicornuta* (Copepoda)	Terazaki et al, 1977
Eukrohnia hamata (Möbius) 1875	Copepoda, mainly *Euchaeta* sp.	Tokioka, 1939
	Copepoda; Ostracoda; Chaetognatha; Radiolaria	Tchindonova, 1959
	Diatomacea, probably obtained with the gulp of water swalled with the prey	Alvariño, 1965
	Herring larvae	Lee, 1966
	Oithona similis, *Metridia pacifica*, *Oncaea borealis*, *Calanus plumchrus* (Copepoda)	Sullivan, 1980
Pterosagitta draco (Krohn) 1853	*Oncaea*, *Corycella*, *Microsetella* (Copepoda); *Sagitta serratodentata* (Chaetognatha)	Stone, 1969
	Oncaea and other Copepoda; Chaetognatha; Tunicata	Newbury, 1978
Sagitta sp.	Fish larvae; *Pseudocalanus*, *Calanus* and other Copepoda; Chaetognatha	Lebour, 1922
	Young fish; Crustacea; Chaetognatha	Bigelow, 1926
	Fish larvae; Copepoda; Crustacea larvae; Salps (Tunicata)	Massuti Oliver, 1954
	Fish larvae; small Crustacea	Hardy, 1956
	Young fish, Copepoda; Chaetognatha	Nicol, 1960
Sagitta bedoti Béraneck 1895	Fish larvae; Copepoda; Crustacea larvae; other zooplankters	Alvariño (unpubished data)
Sagitta bierii Alvariño 1961	Fish larvae; Copepoda; Crustacea larvae; Euphausiidae; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta bipunctata (probably *S. elegans* Verrill 1873)	Herring larvae; *Pseudocalanus elongatus*, *Acartia clausi*, *Temora*	

TABLE IV. Cont.

Species	Food	Author
	longicornis, Centropages, Calanus finmarchicus, Corycaeus anglicus (Copepoda); *Gebia* larvae; Chaetognatha	Lebour, 1922, 1923
Sagitta bipunctata Quoy and Gaimard 1827	*Corycella concinus, Oncaea* (Copepoda)	Stone, 1969
S. bipunctata (probably *S. friderici* Ritter-Zahony 1911)	Fish larvae; *Paracalanus; Clausocalanus, Calocalanus, Centropages, Oithona, Oncaea, Temora, Microsetella, Euterpina* (Copepoda); *Evadne, Podon, Penilia* (Cladocera); Ostracoda; eggs, veliger larvae; Chaetognatha; Dinoflagellates; Diatomacea	Pearre, 1974
Sagitta bruuni Alvariño 1967	Fish larvae; Copepoda; Crustacea larvae; Mollusca larvae; Chaetognatha	Alvariño (unpublished data)
Sagitta crassa Tokioka 1938	*Acartia clausi, A. erythraea, Calanus, Tortanus, Centropages, Paracalanus* (Copepoda)	Murakami, 1959
	Tigriopus japonicus (Copepoda)	Takano, 1971
Sagitta elegans Verrill 1873	*Clupea harengus* larvae	Lebour, 1923
	young fish; Copepoda	Bigelow, 1926; Kuhlmann, 1977
	Calanus finmarchicus (Copepoda)	Wimpenny, 1937
	Fish larvae; *Calanus plumchrus* (Copepoda)	Lee, 1966, 1974
	Nauplii, small Copepoda	McLaren, 1966
	Eggs and fish larvae; *Metridia lucens, Centropages typicus, Calanus finmarchicus, Pseudocalanus elongatus, Paracalanus parbus, Temora longicornis, Centropages hamatus, Acartia clausi, Corycaeus anglicus, Oithona* sp., *Microsetella norvegica, Euterpina acutifrons* (Copepoda); *Podon intermedius, P. leuckarti* (Cladocera); Cirripedia larvae; Euphausiidae; Chaetognatha	Rakuza-Suszczenski, 1969
	Copepoda	Rozanska, 1971; Sameoto, 1972; King, 1979
	Acartia, Pseudocalanus, Oithona, Eurytemora, Tortanus	

TABLE IV. Cont.

Species	Food	Author
Sagitta elegans Verrill 1873 (Cont.)	(Copepoda); Nauplii; Polychaeta; Chaetognatha; *Podon leuckarti*, *Evadne nordmanni* (Cladocera); Tintinnidae; Rotifera	Pearre, 1973, 1981
	Calanus cristatus, *Oithona similis*, *Metridia pacifica*, *Calanus plumchrus* (Copepoda); Chaetognatha	Sullivan, 1980
	Fish larvae; Copepoda; Euphausiidae; Crustacea larvae; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta enflata Grassi 1881	Chaetognatha	Grey, 1930
	Copepoda; Chaetognatha	Furnestin, 1953, 1957
	Fish larvae; Copepoda; Chaetognatha	Suárez-Caabro, 1955
	Fish larve; *Corycaeus*, *Calanus* (Copepoda); *Lucifer*, other Crustacea; Chaetognatha; *Thalia democratica* and other Tunicata	Furnestin, 1957
	Decapod larvae	Wickstead, 1965
	Stephanopyxis palmeriana (Diatomacea)	Almeida Prado, 1968
	Oncaea, *Corycella*, *Eucalanus*, *Corycaeus* (Copepoda)	Stone, 1969
	Chaetognatha	Venter, 1969
	Fish larvae; *Paracalanus*, *Clausocalanus*, *Ctenocalanus*, *Calocalanus*, *Centropages*, *Oithona*, *Oncaea*, *Corycaeus*, *Microsetella*, *Euterpina*, *Temora* (Copepoda); *Evadne*, *Podon*, *Penilla* (Cladocera); other Crustacea; Chaetognatha; Dinoflagellates	Pearre, 1974
	Fish larvae; *Paracalanus*, *Clausocalanus*, *Ctenocalanus*, *Calocalanus*, *Centropages*, *Temora*, *Cadacia*, *Mecynocera* *Acartia*, *Oithona*, *Oncaea*, *Corycaeus*, *Corycella*, *Microsetella*, *Euterpina*, *Sappirina*, *Copelia* (Copepoda); *Evadne*, *Podon*, *Penilla* (Cladocera); Arthropod eggs; Chaetognatha; Appendicularia; Dinoflagellata; Diatomacea	Pearre, 1976
	Copepoda; Chaetognatha; *Oikopleura* (Appendicularia); Cillata	Szyper, 1978

TABLE IV. Cont.

Species	Food	Author
Sagitta enflata Grassi 1881	*Corus julis*, *Serranus hepatus*, *Cepola macrophthalma* fish larvae	Regner, 1980
	Fish larvae; Copepoda; Euphausiidae larvae; Hydromedusae; Siphonophorae; Chaetognatha	Alvariño (unpublished data)
Sagitta euneritica Alvariño 1961	Eggs and larvae of *Engraulis mordax*; *Artemia salina*	V.R. Nair, 1976
	Sardinops caerulea, *Engraulis mordax* larvae; Copepoda; Crustacea larvae; Hydromedusae; Chaetognatha	Alvariño (unpublished data)
Sagitta euxina Moltchanoff 1909	*Calanus helgolandicus* (Copepoda); Cladocera; Crustacea larvae; Chaetognatha	Elian, 1960
	Eggs and fish larvae; Copepoda; Mollusca larvae; Polychaeta; Chaetognatha; Appendicularia	Mironov, 1960
Sagitta ferox Doncaster 1903	Diatomaceas	Nagasawa (in Nagasawa and Marumo 1976)
	Fish larvae; Copepoda; Euphausiidae; Crustacea larvae; Medusae; Siphonophorae	Alvariño (unpublished data)
Sagitta friderici Ritter-Zahony 1911	*Calanus*, *Corycaeus* (Copepoda); *Hyperia* (Amphipoda)	Furnestin, 1957
	Fish larvae	Heydorn, 1959
	Fish-larvae; Copepoda; Cladocera; Amphipoda; Hydromedusae; Appendicularia	Almeida Prado, 1968
	Undinula, *Corycella*, *Corycaeus*, *Centropages* (Copepoda)	Stone, 1969
	Copepoda	Venter, 1969
	Fish larvae; *Paracalanus*, *Clausocalanus*, *Centropages*, *Candancia*, *Oithona*, *Oncaea*, *Corycaeus*, *Microsetella*, *Euterpina* (Copepoda); *Evadne*, *Podon* (Cladocera); Arthropod eggs, Chaetognatha; Appendicularia; Dinoflagellata	Pearre, 1976
	Fish larvae; Copepoda; Medusae	Alvariño (unpublished data)
Sagitta gazellae Ritter-Zahony 1909	*Calanus propinguos*, *Rhincalanus gigas*, *Pleuromamma robusta*, *Metridia gerlachi*, *Calanus* sp., (Copepoda); *Tysanoessa* sp., *T. macrura*, *T. vicina* (Euphausiidae);	

TABLE IV. Cont.

Species	Food	Author
Sagitta gazellae Ritter-Zahony 1909	Amphipoda; *Primo macropa* and other Crustacea; Chaetognatha	David, 1955
	Copepoda; Euphausiidae; Crustacea larvae	Alvariño (unpublished data)
Sagitta hexaptera d'Orbigny 1843	Fish larvae; Copepoda; Chaetognatha	Suárez-Caabro, 1955
	Candacia aethiopica and other Copepoda	Furnestin, 1957
	Oncaea, *Eucalanus*, *Corycella* (Copepoda), Ostracoda; Chaetognatha	Stone, 1969
	Sardina pilchardus, *Engraulis encrasicholus*, *Sardinops caerulea*, *Engraulis mordax*, and other fish larvae, Copepoda; Euphausiidae; Amphipoda; other Crustacea; Hydromedusae; Siphonophorae; Chaetognatha	Alvariño (unpublished data)
Sagitta hispida Conant 1895	Fish larvae; Copepoda; Chaetognatha	Suárez-Caabro, 1955
	Fish larvae; Copepoda; *Lucifer* and other Crustacea; Medusae; Siphonophorae; Chaetognatha; Appendicularia	Furnestin, 1957
	Artemia nauplii; other *S. hispida* (under laboratory conditions)	Reeve, 1964
	Fish larvae; *Corycaeus giesbrechti* (Copepoda); *Penilia avirostris* (Cladocera); Amphipoda; *Liriope tetraphylla* (Medusae); Chaetognatha; Appendicularia	Almeida Prado, 1968
	Acartia tonsa, *Oithona nana* (Copepoda); Chaetognatha	Reeve and Walter, 1972
	Copepoda	Reeve et al, 1975
	Copepoda; Chaetognatha	Alvariño (unpublished data)
Sagitta lyra Krohn 1853	Copepoda; Ostracoda	Tchindonova, 1959
	Oncaea (Copepoda)	Stone, 1969
	Copepoda	Venter, 1969
	Fish larvae; Copepoda; Euphausiidae; Amphipoda; Crustacea larvae; Medusae;	

TABLE IV. Cont.

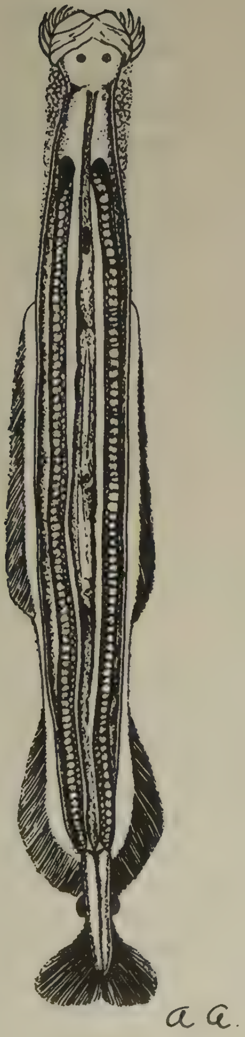
Species	Food	Author
	Siphonophorae; Chaetognatha	Alvariño (unpublished data)
Sagitta macrocephala Fowler 1905	Chaetognatha	Tchindonova, 1959
	Calanus pacificus, *Lucicutia bicornuta* (Copepoda)	Terazaki et al, 1977
	Copepoda	Alvariño (unpublished data)
Sagitta maxima (Conant) 1896	*Euchaeta* (Copepoda); Amphipoda; *Tomopteris* (Polychaeta); Chaetognatha	Bigelow, 1926
	Fish larvae	Lee, 1966
	Fish larvae; Copepoda; Euphausiidae; Crustacea larvae	Alvariño (unpublished data)
Sagitta minima Grassi 1881	Copepoda	Venter, 1969
	Paracalanus, *Clausocalanus*, *Ctenocalanus*, *Calocalanus*, *Oithona*, *Centropages*, *Oncaea*, *Corycaeus*, *Microsetella*, *Euterpina* (Copepoda); *Evadne*, *penilia* (Cladocera); Crustacea larvae; veliger larvae; invertebrate eggs; Chaetognatha	Pearre, 1974, 1976
	Small Copepoda; Invertebrate larvae	Alvariño (unpublished data)
Sagitta nagae Alvariño 1967	*Candacia pinnata*, *Calanus pacificus*, *Pareuchaeta russelli* (Copepoda)	Nagasawa and Marumo, 1972
	Calanus pacificus, *Corycaeus affinis*, *C. dahli*, *C. dubius*, *Clausocalanus arcuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus* (copepoda)	Nagasawa and Marumo, 1976
	Fish larvae; Copepoda; Crustacea larvae; Hydromedusae; Mollusca larvae	Alvariño (unpublished data)
Sagitta pacifica Tokioka 1940	Copepoda; Hydromedusae; Chaetognatha	Alvariño (unpublished data)
Sagitta pulchra Doncaster 1903	Fish larvae; Copepoda; Crustacea larvae; Polychaeta larvae	Alvariño (unpublished data)
Sagitta robusta Doncaster 1903	*Corycella*, *Oncaea*, *Microsetella*, *Candacia*, *Corycaeus* (Copepoda)	Stone, 1969

TABLE IV. Cont.

Species	Food	Author
	Fish larvae; Copepoda; Crustacea larvae; Euphausiidae	Alvariño (unpublished data)
Sagitta scrippsae Alvariño 1962	Fish larvae; Copepoda; Euphausiidae; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta serratodentata Krohn 1853	*Calanus* (Copepoda)	Furnestin, 1957
	Undinula, *Corycella*, *Centropages* (Copepoda)	Stone, 1969
	Copepoda; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta setosa Müller 1847	*Calanus finmarchicus* (Copepoda); Diatomacea	Wimpenny, 1937
	Clupea harengus larvae; Copepoda	Parry, 1944
	Fish larvae; *Paracalanus*, *Acartia*, *Oithona*, *Centropages*, (Copepoda); Cladocera; Ostracoda; Crustacea larvae; Polychaeta larvae; Chaetognatha; Appendicularia	Mironov, 1960
	Clupea harengus eggs and larvae; *Isias clavides*, *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Centropages anglicus*, *Microsetella norvegica*, (Copepoda); *Podon intermedius*, *P. leuckarti* (Cladocera); *Themisto abyssorum* (Amphipoda); Appendicularia	Rakusa-Suszczensk 1969
	Fish larvae; *Pseudocalanus elongatus* and other Copepoda	Kuhlmann, 1977
	Sardina pilchardus larvae; Copepoda; microplankton	Alvariño (unpublished data)
Sagitta tasmanica Thomson 1947	Copepoda	Venter, 1969
	Fish larvae; Copepoda; Amphipoda; Euphausiidae; Medusae	Alvariño (unpublished data)
Sagitta tokiokai Alvariño 1967	Copepoda; Euphausiidae	Alvariño (unpublished data)
Sagitta zetesios Fowler 1905	*Calanus pacificus*, *Pareuchaeta russelli*, *Eucalanus subtenuis*, *Euchaeta concinna* (Copepoda); *Conchoecia elegans* (Ostracoda); *S. nagae*, *S. zetesios* (Chaetognatha)	Terazaki (in Nagasawa and Marumo 1976)
	Calanus cristatus, *C. pacificus*,	

TABLE IV. Cont.

Species	Food	Author
Sagitta zetesios Fowler 1905 (Cont.)	*Calanus plumchrus, Undinula vulgaris, Eucalanus ngii, E. crassus, E. subtenuis, Rhincalanus cornutus, R. nasutus, Clausocalanus arcuicornis, Aetideus armatus, Gaetanus Armiger, Euchaeta concinna, Pareuchaeta russelli, P. scaphula, P. rubra, Scaphocalanus echinatus, Scolecithrix danae, S. nicobarica, Scolecithricella valida, Pleuromamma abdominalis, Heterorhabdus pacificus, Candacia bipinnata, Oncaea conifera* (Copepoda); *Sagitta nagae, S. lyra, S. decipiens, S. macrocephala, S. zetesios* (Chaetognatha); *Conchoecia elegans* (Ostracoda)	Terazaki and Marumo, 1982



CHAETOGNATHA: *Sagitta scrippsae* **Alvariño 1962**

OTHER ZOOPLANKTON PREDATORS ON FISH LARVAE AND SOME ZOOPLANKTER COMPETITORS FOR FOOD WITH FISH LARVAE.

COPEPODS

Revision of studies conducted by various biologists (as reviewed in Russell 1931) regarding food of fish, shows the importance of free-swimming copepods in the economy of living marine organisms. All fishes of commercial importance feed on Copepoda at some time of their life cycle, and certainly at least during their early stages of development. Pelagic species, such as sardine, anchovy, herring, and mackerel, (probably the most successful of fish populations) feed directly on Copepoda. Therefore, Copepoda constitute the main connection in the complicate web between the diatoms and the carnivores. Indeed, the abundance of copepods concurred with highest concentration of anchovy larvae (Alvariño 1979, 1980b) in the California region.

Copepods are distributed into three categories of feeding characteristics (Esterly 1916; Lebour 1922, 1923; Wickstead 1962) based on examination of the stomach content and structure of mouth parts. These include diatom feeders, omnivores, and carnivores. The observed foods of Copepoda and other predatory Crustacea, Mollusca, and Annelida in the plankton realm are listed in Table VI.

Several marine copepods have been observe to fatally injure, capture or ingest young fish and fish larvae during laboratory experiments. Species of Copepoda common in the surface waters of the California Current, *Labidocera jollae*, *L. trispinosa*, and *Pontellopsis occidentalis*, appear to show some predation on fish larvae (Lillelund and Lasker 1971). These copepods may detect and react to vibrations produced by the larvae tail beat by capturing and biting the larvae. Young anchovy larvae are more vulnerable to predation by these copepods, but when the swimming ability of the anchovy increases with age, the copepods are less effective fish larvae feeders or attackers. *P. occidentalis* was able to kill anchovy up to three and a half day-old (Lillelund and Lasker 1971), and the authors explain that "although capture and ingestion of fish larvae was a common fact under laboratory conditions, it is rare to find a copepod with a captured fish larvae in Formalin-preserved plankton". The copepod *Labidocera trispinosa* occurs in the upper 10 m of the California Current, strata which are also occupied by the larvae of *Engraulis mordax*, *Sardinops caerulea*, *Scomber japonicus*, *Trachurus symmetricus*, and *Cololabis saira*, but a quantitative relation between these copepods and the fish larvae has not been analyzed in nature. During experiments by Lillelund and Lasker (1971) the additional *Artemia* larvae included as an alternate prey decreased the feeding of *L. trispinosa* on the fish larvae. The laboratory observations indicate "that marine copepods may be effective predators on larval fish, at least in the sense that a predator need not devour its prey but is equally effective if it injures it mortally".

Experiments rearing fish larvae of *Blennius ocellaris* show (Garstand 1900) they were devoured by Harpacticoid copepods, mainly *Idia furcata*, which had entered the aquarium system; the rapacity of these copepods indicate they attacked healthy 25 mm long young *Gobius minutus* and fed indiscriminately on live, moribund, and dead *Blennius* larvae. The omnivorous copepod *Temora longicornis*, *Centropages typicus*, *Calanus finmarchicus*, and *Labidocera wollastoni* were fed on a mixed diet of copepods and diatoms (Lebour 1922), and the carnivorous *Anomalocera patersoni* fed on other copepods and fish larvae (Lebour 1923). Examination of digestive content of carnivorous Copepoda, *Labidocera*, *Anomalocera*, *Centropages*, *Euchaeta*, and *Candacia* showed they feed mainly on other copepods (Gould 1966). The copepod *Candacia bradyi* commonly found in the Singapore region (Wickstead 1959) was observed eating *Sagitta enflata* (the most abundant Chaetognatha in that region); however, no data have been published on its feeding on fish larvae, which would probably take place if they are abundant in the locations inhabited by *C. bradyi*. Females of the carnivorous copepods *Candacia aethiopica* have been observed (Wickstead 1965) sizing Myctophid fish larvae.

The study by Samyshev (1973) of the phytophagous, predatory and euryphagous copepods from the Gulf of Guinea, indicates that predatory copepods reach the 80 % of the total copepods - biomass in the 500-299 m layers, 35 % at the 200-100m, and 40 % at 100-0 m depth, and considers that the relation of phytophagous copepods to predators in the upper 100 m layer at the zone of divergence could be dependent on the rate of upwelling in the Equatorial region. The carnivorous copepods in the region included, *Oncaea* sp., *Oithona* sp, *Euchaeta marina*, *E. paraconcinna*, *E. hebes*, *Euchaeta* sp., *Paraeuchaeta* sp., *Microsetella gracilis*, *M. rosea*, *Corycaeus* sp., *Euchaeta marina* considered one of the most predatory of copepods, but no information was provided on the prey consumed. Deep sea adult copepods from the Sargasso Sea, *Euchaeta media*, *E. norvegica*, *E. tumidula*, *Euchaeta* sp., *Heterorhabdus abyssalis*, *H. compactus*, *H. norvegi*-

ca, *Euaugaptilus* sp., contained only crustacea remains in their guts (Harding 1974). The digestive tracts of *Pseudochirella polyspina* and *Scaphocalanus magnus* (from the slope waters off Nova Scotia) contained remains of Euphausiids and Copepoda.

EUPHAUSIIDS

Some species of Euphausiidae are omnivorous or carnivorous. The euphausid *Meganyctiphanes norvegica* was observed by Holt and Tattersall (1905) to feed upon fish larvae, Decapoda larvae, and Heteropoda. Euphausiids of the Gulf of Maine feed chiefly on phytoplankton, but *M. norvegica* were observed clasping bits of herring refuse from the packing factories (Bigelow 1926) and feeding on young fish and copepods; specimens were also found with masses of the diatom *Rhizosolenia* in their stomachs. *M. norvegica* from Loch Fyne fed on *Calanus finmarchicus*, *Paraeuchaeta norvegica*, eucaridean species, other euphausiids, dinoflagellates, diatoms, fern sporangia, detritus, algae, and dipteran eggs. Cannibalism occurred when the proportion of euphausiids to other organisms in the plankton was high (Fisher and Goldie 1959).

Laboratory studies by Theilacker and Lasker (1973) on *Euphausia pacifica* and *Engraulis mordax* larvae, the most abundant Euphausiidae and Clupeidae, respectively, in the California Current region, appear to indicate that "the average number of anchovy larvae, juvenile euphausiids can process in a day catching, eating, digesting, and excreting is 10 or less. Increasing the prey concentration above this number had no effect on feeding in the volumes tested". The authors indicate that the results "suggest a constant feeding rate with food not a limiting factor". Theilacker and Lasker (1973) observed that the amount of feeding was not affected by the addition of more prey items and that increased larval activity decreased the ability of *E. pacifica* to capture anchovy larvae. *E. pacifica* exhibited a 60 % successful catch rate when dealing with one day (newly hatched) and 2 day-old larvae, but the capture rate diminished to 17 % for the three day-old larvae, and to 11 % for 4 day-old larvae. *E. pacifica* ingested few eggs in the laboratory, possibly due to either the eggs being unavailable to the euphausiids (eggs float at the surface of waters) or produce no vibrations in the water, which would atract euphausiids. Thailacker and Lasker (1973) calculated that the number of fish larvae

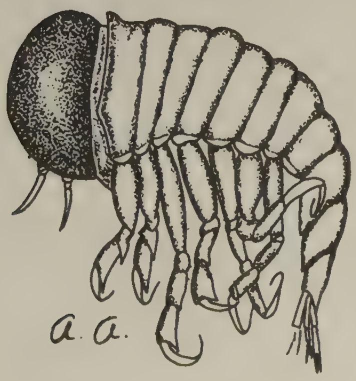
E. pacifica could consume daily per m^2 surface was 2.847, regardless of the presence of other zooplankters.

Chlorophyll pigments have been found in considerable amounts in the stomachs of such omnivorous or carnivorous euphausiid species as *Nematoscelis gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, *N. difficilis* and *Euphausia pacifica*. Work on these findings will indicate these pigments may have some physiological role in the metabolism of euphausiids, or are totally removed from the system during defecation.

AMPHIPODS

The Amphipoda *Euthemisto* sp. prey upon small planktonic animals in the Gulf of Maine (Bigelow 1926); although it was not observed feeding on young fish, their stomachs have been found to be packed with copepods (mainly *Calanus* and *Temora*), pieces of other crustaceans, and fish eggs.

The observed food in Copepoda and other predatory Crustacea are listed in Table V.



AMPHIPODA: *Hyperoche medusarum* **Krøyer 1838**

TABLE V. OBSERVATIONS ON THE FOOD OF PELAGIC CRUSTACEA

CLASS: ORDER Species	Food	Author
CRUSTACEA: COPEPODA		
Acanthocyclops vernalis (Robertson and Gannon) 1981	*Notropis hudsoni* fish larvae	Harting, Jude and Evans, 1982
Acartia clausi Giesbrecht 1889 Sulcanus conflictus Nicholls 1944	*Gladioferens imparipes* and other Copepoda	Hodgkin and Rippindale 1971; Rippindale and Hodgkin, 1974
Acartia tonsa Dana 1849	*Scottolana canadensis*, *Oithona colcarva*, *Eurythemora affinis*, *Acartia tonsa* nauplii (Copepoda)	Lonsdale et al, 1979.
Anomalocera pattersoni Templeton 1837	Copepoda, fish larvae	Lebour, 1922, 1925
Anomalocera sp. *Candacia* sp. *Centropages* sp. *Euchaeta* sp. *Labidocera* sp.	Copepoda	Gould, 1966
Calanus finmarchicus (Gunnerus) 1765 *Centropages typicus* Kroyer 1849 *Labidocera wollastoni* Giesbrecht 1892 *Temora longicornis* (Müller) 1792	Copepoda	Lebour, 1922
Calanus pacificus Brodsky 1948	Copepoda nauplii and copepodites; Phytoplankton	Landry, 1981
Candacia sp.	Sardine post-larvae	Karlovack, 1967
Candacia bradyi Scott 1904	Copepoda; Chaetognatha; other zooplankters	Wickstead, 1959
Candacia aethiopica Dana 1849	Fish larvae	Wickstead, 1965
Candacia columbiae Campbell 1929	Medusae; Crustacea	Gould, 1966
Corycaeus flaccus Giersbrecht 1891	Post larval fish *Electrona rissoi*	Regner, 1980
Cyclops bicuspidatus Thomasi-*Diacyclops thomasi* (Robertson and Gannon) 1981	*Morone saxalis* (striped bass), *M. americana* (white perch) larvae	Smith and Kerneham, 1981
	Alosa pseudoharengus and *Notropis hudsoni* fish larvae	Harting, Jude and Evans, 1982
Euaugaptilus sp.	Crustacea	Harding, 1974
Euchaeta elongata Esterly 1913	*Aetideus divergen*, *Pseudocalanus spp.*,	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
	Paracalanus parvus, *Oithona similis* (Copepoda); *Artemia* nauplii	Yen, 1982
	Merluccius productus (hake) eggs and larvae	Bailey and Yen, 1983
Euchaeta media Giesbrecht 1888	*Calanus*; other Crustacea	Brooks, 1970
Euchaeta norvegica Boeck 1872	*Acartia tonsa*, *Centropages hepatus* (Copepoda)	Conover, 1960
Euchaeta tonsa Giesbrecht 1895	*Calanus* nauplii, *Eucalanus* copepodites	Brooks, 1970
Idya furcata=*Tisbe furcata* (Baird) 1837	Fish larvae	Garstand, 1900
Labidocera jollae Esterly 1906 *Labodocera trispinosa* Esterly 1905 *Pontellopsis occidentalis* Esterly 1906	Fish larvae	Lillelund and Lasker, 1965
Labidocera trispinosa Esterly 1905	*Labidocera* nauplii, *Acartia tonsa*, *Paracalanus*, *Calanus* sp. (Copepoda)	Landry, 1978
Oithona nana Giesbrech 1892	Copepoda nauplii	Lampitt, 1978
Pleuromamma quadrangulata (Dahl) 1893	*Rhincalanus* nauplii	Brooks, 1970
Pseudochirella polyspina Brodsky 1950		
Scaphocalanus magnus (T. Scott) 1894	Euphausiidae	Harding, 1974
Sapphirina angusta Dana 1849	*Thalia democratica* (Tunicata)	Heron, 1973
Temora stylifera (Dana) 1849	*Gobius* sp. fish larvae	Regner, 1980
Tortanus discaudatus Thompson and Scott) 1897	*Calanus pacificus* (Copepoda)	Ambler and Frost, 1974
: EUPHAUSIIDAE		
Bentheuphausia amblyops G.O. Sars 1885	Copepoda; Medusae; Chaetognatha; Radiolaria; Tintinnidae; Phytoplankton	Tchindonova, 1959
Euphausia pacifica Hansen 1911	Eggs and fish larvae	Theilacker and Laske 1973
Megancyctiphanes norvegica (M. Sars) 1857	Young fish; Copepoda; Euphausiidae; Decapoda larvae; Heteropoda	Holt and Tattersal, 1905
	Fish; Copepoda; Diatomacea	Bigelow, 1926
	Calanus finmarchicus, *Euchaeta*	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
	norvegica, *Pseudocalanus elongatus*, *Acartia clausi*, *Oithona helgolandica* (Copepoda); Dinoflagellata; Silicoflagellata; Diatomacea	Macdonald, 1927
	Copepoda; other Crustacea; Dinoflagellata; Diatomacea; detritus	Fisher and Goldie, 1959
	Artemia salina (under laboratory conditions)	Heyrand, 1979
	Copepoda; *Chaetoceros atlanticus*; Phytoplankton	Sameoto, 1980
Nematobrachion sp.	Copepoda	Nemoto, 1972
Nematobrachion boopis (Colman) 1896	Copepoda	Roger, 1973
Nematobrachion sexpinosus Hansen 1911	Fish larvae; *Pleuromamma*, *Oithona* (Copepoda); Euphausiidae; Decapoda Crustacea; Chaetognatha	Hu, 1978
Thysanopoda aequalis Hansen 1905	Fish larvae; *Pleuromamma*, *Oithona* (Copepoda); Euphausiidae; Decapoda Crustacea; Chaetognatha	Hu, 1978
Thysanopoda cornuta Illig 1905	Copepoda; Medusae; Chaetognatha; Radiolaria	Tchindonova, 1959
	Fish larvae; Copepoda; Euphausiidae; Amphipoda; Decapod larvae; other Crustacea; Mysidacea; Chaetognatha; Radiolaria	Nemoto, 1977
Thysanopoda cristata G.O. Sars 1885	Copepoda	Roger, 1973
Thysanopoda egregia Hansen 1905	*Cyclothone* and other fish larvae; Copepoda; Euphausiidae; Mysidacea; Chaetognatha; pelagic Cephalopoda; Radiolaria	Nemoto, 1977
Thysanopoda monocantha Ortman 1893	Juvenile fish	Roger, 1973
	Fish larvae; *Pleuromamma*, *Oithona* (Copepoda); Euphausiidae; Decapod Crustacea; Chaetognatha	Hu, 1978
Thysanopoda orientalis Hansen 1910 *Thysanopoda pectinata* Ortman 1893 *Thysanopoda tricuspidata* Milne-Edwards 1837	Juvenile fish	Roger, 1973
Thysanopoda spinicaudata Brinton 1953	Fish larvae; Chaetognatha	Nemoto, 1977
Thysanoessa inermis (Krøyer) 1846	Copepoda; *Chaetoceros*	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
Thysanoessa inermis (Krøyer) 1846 (Cont.)	*atlanticus*; Plytoplankton	Sameoto, 1980
Thysanoessa raschii (M. Sars) 1840	Copepoda	Sameoto, 1980
:MYSIDACEA		
Mysidopsis bigelowi Tattersall 1926 *Neomyopsis americana* (S.I. Smith) 1873	*Acartia tonsa*, *Centropages* sp. *Pseudocalanus coronatus*, *Paracalanus crassirostris*, *Oithona colcarra* (Copepoda)	Fulton, 1982
Mysidopsis didelphys Norman 1906	Copepoda	Mauchline, 1970
Mysidopsis gibbosa G.O. Sars 1885	Copepoda; Dinoflagellata	Mauchline, 1970
Neomysis mercedis (Holmes)	*Eurithemora hirundoides*, (Harpacticoid Copepoda)	Siegfried and Kopache, 1980
:ISOPODA		
Rocinela belliceps pugettensis	Juvenile Pacific Salmon	Novotny and Mahnken, 1971
:CLADOCERA		
Podon intermedius Lilljeborg 1901	*Gobius* fish larvae	Regner, 1980
:OSTRACODA		
Conchoecia alata Müller 1906	Crustacea; Tintinnida; Radiolaria, Coccolithophorida; Foraminifera; Silicoflagellates; Diatomacea	Tchindonova, 1959
Conchoecia ametra Müller 1906	Crustacea, Tintinnida; Radiolaria, Coccolithophorida	Tchindonova, 1959
Conchoecia atlantica (Lubbock) 1865 *Conchoecia rhynchena* Müller 1906 *Conchoecia secernenda* Vavra 1906	Crustacea	Angel, 1970,1972
Conchoecia bispinosa Claus 1890 *Conchoecia echinata* Müller 1906	Crustacia; Diatomacea	Iles, 1961
Conchoecia borealis Sars 1865 *Conchoecia elegans* Sars 1865 *Conchoecia obtusata* Sars 1865	Crustacea	Elofson, 1941
Conchoecia skogsbergi Iles 1953	Coccolithophora; Foraminifera; Silicoflagellata; Diatomacea	Angel, 1970, 1972
Conchoecia spinirostris Claus 1874	Myctophid fish; Crustacea; Chaetognatha; Tintinnida; Radiolaria; Coccolithophorida; Foraminifera; Silicoflagelata; Diatomacea	Angel, 1970, 1972

TABLE V. Cont.

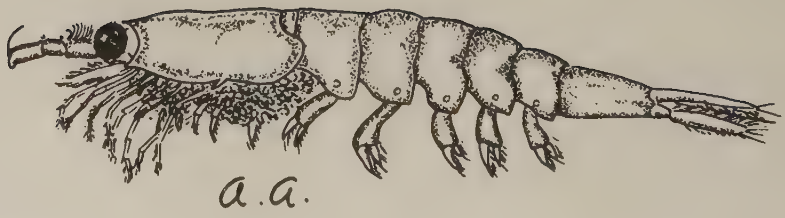
CLASS: ORDER Species	Food	Author
:AMPHIPODA		
Anomys sp.	Pteropoda; *P. pacifica* and other Amphipoda	Fukuchi, Yoshida, Hara, 1971
Calliopius sp.	*Clione limacina* (Pteropoda)	Fukuchi, Yoshida, Hara, 1971
Euthemismo sp.	Fish eggs; *Calanus*, *Temora* (Copepoda); Euphausiidae; Amphipoda; Decapod larvae	Bigelow, 1926
Euthemisto compressa = *Themisto gaudichaudi* Guérin-Méneville 1825	Copepoda; Euphausiidae	Conover, 1960
Hyperia galba (Montagu) 1813	Copepoda; Mollusca	Conover, 1960
Hyperoche medusarum (Krøyer) 1837	*Clupea pallasi* and flat fish larvae	Westernhagan and Rosenthal, 1976
Parathemisto gaudichaudi (Guerin) 1836	Copepoda; Euphausiidae; Diatomacea	Nemoto and Yoo, 1970
	Clupeidae, *Ammodytidae* fish larvae; *Acartia*, *Temora*, *Anomalocera*, *Calanus* (Copepoda); *Nyctiphanes cauchi*, *Thysanoessa inermis*, *T. raschii*, *Meganyctiphanes norvegica* (Euphausiidae); *Sagitta elegans* (Chaetognatha); Amphipoda; *Aequorea vitrina*, *A. aequorea* (Medusae) and larvae of other Invertebrates	Sheader and Evans, 1975
Parathemisto japonica Bovallius 1887= *Themisto japonica*	*Metridia* and other copepoda; Euphausiidae; Ostracoda; Medusae; Foraminifera; Radiolaria; Tintinnidae	Zhuravlev and Neyman, 1976
	Ammodytes personatus fish larvae	Yamashita and Joh (Communication)
Parathemisto libellula (Lichtenstein) 1822= *Themisto libellula*	Cod larvae	Lee, 1966
Parathemisto pacifica = *Themisto pacifica* (Stebbing) 1888	*Clione limacina* (Pteropoda); *P. pacifica* and other Amphipoda	Fukuchi, Yoshida, Hara, 1971
Pseudolibrotus sp.	Cod larvae	Lee, 1966
:DECAPODA		
Penaeus aztecus (Ives) 1891		
Penaeus brasiliensis Latreille 1817		
Penaeus duorarum Burkenroad 1939		

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
Penaeus kerathurus Forskal 1775	Fish larvae; Eupahusiidae; Amphipoda; other Crustacea; Polychaeta; Echinodermata	Burukovskyi and Froyerman, 1973
Sergestes similis Hansen 1903	Copepoda; Euphausiidae; Tintiniidae	Tchindonova, 1959; Renfro and Pearcy, 1966
Sergestes lucens Hansen 1903	Fish; *Calanus pacificus*, *Paracalanus parvus*, *Euchaeta marina*, *Candacia* sp, *Oncaea venusta*, *Clausocalanus arcuicornis*, *Mondilla typica*, *Pareuchaeta ruselli*, *Pleuromamma gracilis*, *Oithona plumifera*, *Gaetanus* *Euchirella* sp.(Copepoda); Chaetognatha; Mollusca; Diatomacea	Omori, 1969
Sergestes japonicus Bate 1881	Fish; Copepoda; Chaetognatha	Tchindonova, 1959
Decapod larvae	Young fish; small Crustacea	Steuer, 1910; Bigelow, 1926
Homarus americanus Milne-Edwards 1837 (larvae)	Other Crustacea	Weldon and Fowler, 1890
Homarus vulgaris Linnaeus 1758 (larvae)	Decapod larvae; Copepoda	Lebour, 1922
Palinurus vulgaris = *Palinurus elephas* Fabricius 1787	*Lophius piscatorius* larvae; Copepoda	Lebour, 1925
Squilla desmaresti= *Meiosquilla desmaresti* (Risso) 1816	*Temora longicornis* (Copepoda); Crustacea	Lebour, 1925
Phyllosoma of *Jasus lallandei*	Hydromedusae	Williamson (in Thomas, 1963)
Phyllosoma of *Scyllaridae*, *Scyllarus americanus* (S.I. Smith) 1869, *Scyllarus chacei* Holthuis 1960	*Liriope tetraphylla* (Medusae)	Shojima, 1963; Herrnkind et al 1976
Hymenodora frontalis Rathbum 1902	Fish larvae; Copepoda; Other Crustacea; Medusae; Chaetognatha; Tintinnidae	Tchindonova, 1959
Hymenodora glacialis S.I. Smith 1886	Copepoda; Amphipoda; Ostracoda; other Crustacea; Medusae; Polychaeta; Chaetognatha; Radiolaria	Tchindonova, 1959
Gennadas borealis Rathbum 1902	Copepoda; other Crustacea; Medusae; Chaetognatha;	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
	Radiolaria; Tintinnidae	Tchindonova, 1959
Physetocaris microphthalma	Copepoda; Ostracoda; Chaetognatha; Tintinnidae	Tchindonova, 1959
Acanthephyra sp.	Fish; other Crustacea	Tchindonova, 1959
Pasiphaea sp.	Fish; other Crustacea; Tintinnidae	Tchindonova, 1959



EUPHAUSIACEA: *Euphausia pacifica* **Hansen 1911**

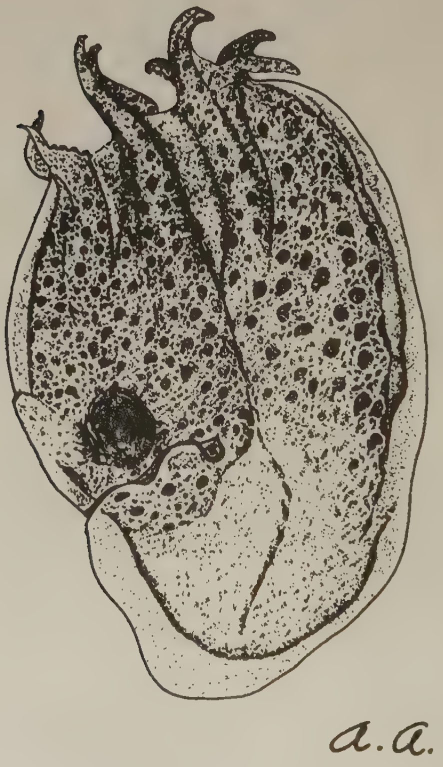
Information on the prey off of Pelagic mollusca appears compiled in Table VI.

CEPHALOPODS

Cephalopoda predation on young fish can have a drastic effect on some fisheries. Johnson (1942) described the behavior of *Paraoctopus apollyon* feeding on small fish and shrimps in Friday Harbor. The octopus obtained food by gliding forward with the tentacles extended in a canopy under which fish and shrimps are captured; contracting the tentacles, the catch is forced slowly into the mouth. The octopus repeated this process in a rapid succession, making 15 of these hauls in twenty minutes.

The squid *Ommatostrephes todaratus* was observed by Hjory and Dahl (1900) as reported in Murray and Hjort (1912), pursuing the herring in Norwegian waters. Those authors explained that these squids "generallly appear in enormous shoals coming from the open ocean in pursuit of the herring shoals on which they gorge themselves greedly". The coincidence of great quantities of *Ommatostrephes* sp. together with several hydromedusae (Lucas and Henderson 1936) coincided with the breakdown of the Shetland herring fishery during 1931.

Octopus vulgaris, *Loligo vulgaris* and *Sepia officinalis hierredda* appeared in great abundance (Cort and Pérez-Gándaras 1973) in the Sahara Bank during 1966-1967 in a region about 50m deep, off the Spanish Sahara. The Sparids *Dentex dentex*, *D. canariensis*, *Pagrus pagrus* and other fish used to be extremely abundant in that region, but this abundance has decreased drastically since 1960 due to overfishing. Coincident with this condition, the population of cephalopods in the region has increased due to lack of natural predators. Thus the abundant cephalopod population will be preying on the young and larvae of Sparidae, preventing these populations from regaining strength. Examination of stomach contents of cephalopods in this area indicated that they feed on young Pleuronectidae, Sparidae, Mollusca, and Crustacea. However, in the far offshore adjacent region off Spanish Sahara, large Sparidae, *Trachurus trachurus*, and *Scomber scombrus* were abundant and preyed on Cephalopoda larvae. In this manner, the cephalopod populations are controlled by the predatory activity of Sparidae and other fish populations. In the Sahara Bank region the depleted Sparidae populations do not harm the Cephalopoda larvae, and so the great number of squids and Octopoda devour the young and larval fish occurring in the region. It appears that the fish population can only be limited by scarcity of food and by the fishery. A cephalopod fishery has started to develop in the Sahara region, and it is expected that it will help to restore the predatory/prey equilibrium. Similarly, absence or scarcity of *Panulirus regius* (spiny lobster) off Sahara (Maigret 1976) coincided with abundance of *Octopus vulgaris* and *Sepia officinalis*.



CEPHALOPODA, OCTOPODA: *Alloposus mollis* **Verrill 1880**

TABLE VI. OBSERVATIONS ON THE FOOD OF PELAGIC MOLLUSCA

CLASS: ORDER Species	Food	Author
GASTROPODA: HETEROPODA		
Heteropod spp.	Fish larvae; Ctenophora; *Phronima* sp. (Hyperiidae); Salps (Tunicata)	Tesch, 1949
Cardiapoda placenta (Lesson) 1830	Fish larvae; *Phyllirhoe atlanticum* (Nudibranchia) *Firoloida desmaresti* (Heteropoda); *Salpa cylindrica* (Tunicata)	Hamner et al, 1975
Pterotrachea coronata Forskal 1775	Physonectae bracts (Siphonophorae)	Hamner et al, 1975
Carinaria cristata f. japonica Spoel 1972	*Myctophidae* fish larvae; *Nematoscelis difficilis*, *Euphausia recurva* (Euphausiidae); *Hyperia* sp., *Phronima Sedentaria* (Amphipoda); *Conchoecia spinosa* (Ostracoda); *Muggiaea atlantica*, *Stephanomia bijuga*, *Nectodroma* sp., and other Siphonophorae; *Tomopteris elegans* (Polychaeta); Chaetognatha; *Limacina*, *Carinaria japonica* (Pteropoda); *Atlanta gaudichaudi* (Heteropoda); *Thalia democratica*, *Doliolum denticulum* Thaliacea); *Oikopleura* sp. (Appendicularia)	Seapy, 1980
Carinaria sp.	*Sardina ocellata* fish eggs and other fish larvae; Crustacea; Scyphozoa Medusae	Graham, 1955
Carinaria japonica Okutani 1955	*Paracalanus parvus*, *Calanus* sp., *Oithona plumifera* (Copepoda); Euphausiid larvae; juvenile Amphipoda; *Evadne* sp. (Cladocera); *Sagitta nagae* (as *S. bedoti*) (Chaetognatha); *Thalassiotrix longisima*(Diatomacea)	Okutani, 1961
: GYMNOSOMATA		
Clione limacina (Phipps) 1774	*Limacina (Spiratella) helicina*, *Spiratella retroversa* (Pteropoda)	Conover and Lalli, 1974
CEPHALOPODA: OCTOPODA		
Octopus vulgaris Cuvier 1797	Fish larvae; Euphausiidae; other Crustacea; Cephalopoda	Burukovskyi and Froyerman, 1973; Cort and Pérez-Gándaras, 1973
Paraoctopus apolyon = *Octopus apollyon* (Berry) 1912	Fish larvae; Decapod Crustacea	Johnson, 1942
:DECAPODA		
Illex coindeti (Verany) 1837		

TABLE VI. Cont.

CLASS: ORDER Species	Food	Author
Todarotes sagittatus (Lamarck) 1979		
Loligo pealei Lesueur 1821	Larvae and juvenile fish; Euphausiidae; crabs and other Crustacea; Cephalopoda	Burukovskýi and Froyerman, 1973
Loligo opalescens Berry 1911	*Scomber japonicus* larvae; adult *Artemia* (Crustacea)	Hurley, 1976
	Fish; Copepoda; Euphausiidae; Amphipoda; Cumacea; Mysidacea; Ostracoda; other Crustacea; Gastropoda; Polychaeta; Cepahlopoda; Radiolaria	Karpov, 1979
Loligo vulgaris Lamarck 1822		
Sepia officinalis hierredda Rang 1837	Fish larvae; Crustacea; Mollusca	Cort and Pérez-Gándaras, 1973
Symplectoteuthis [*Stenoteuthis*] *oualaniensis* (Lesson) 1830	Young fish; Crustacea; Cephalopoda	Filipova, 1974
	Myctophidae fish, flying fish and other fish; Crustacea; Squids	Neis, 1977
Symplectoteuthis luminosa Sasaki 1915		
Ommastrephes bartrami (Lesueur) 1821		
Ommastrephes pteropus (Steenstrup) 1885		
Todarotes angolensis Adam 1962	Young fish; Crustacea; Cephalopoda	Filipova, 1974

OTHER PREDATORY ZOOPLANKTERS

Predation by fish is not considered in this work. Other predatory planktonic organisms are the pelagic worms. Little is known on the feeding characteristics of these animals, and the few observations on the food of pelagic Polychaeta appear compiled in Table VII.

TABLE VII. FOOD OF PELAGIC WORMS

CLASS: ORDER Species	Food	Author
ANNELIDA: POLYCHAETA		
Tomopteris sp.	Young herring; *Agalma elegans* (Siphonophorae)	Akesson, 1962
	Chaetognatha	Uschkov, 1972
Tomopteris helgolandica Greeff 1879	*Clupea harengus* and other fish larvae; Chaetognatha; Unicellular organisms	Lebour, 1923
Typhloscolex mulleri Bush 1851	Chaetognatha	Fernández Alamo (personal communication)

SUMMARY

The data gathered on the food of carnivorous zooplankters, together with observations on the failure of year-class of fish coincident with great abundance of predatory planktonic organisms, indicate that it is paramount for fisheries research to systematically analyze plankton, as food as well as plankton predators. Studies should be increased on the feeding of various fish larvae and carnivorous zooplankters, together with determinations on the voracious capacity of each of the plankton predator species related to the fish larvae. Larval fish and their basic food are greatly utilized by the planktonic carnivores, a factor which contributes to the source of mortality directly by predation, and indirectly by competition for food when the predators consume food of larvae available in the ocean. Continuous monitoring by oceanic surveys on the spawning region of fish and other invertebrates of commercial interest should be accomplished together with the qualitative and quantitative distribution of food and predatory zooplankters.

The study of long and short-term fluctuations in the abundance and distribution of zooplankters (Glover et al 1961) appears to hold a considerable promise to detect and analyze physico-chemical-biological changes in the environment, and consequently in the commercial fish stocks, as well as the effect of predation on the abundance of recruits to integrate the fish stocks. Once this multiple facies of research is properly achieved (Hardy 1956) "can we safely think of trying to predict the effect of such changes in the fishery".

BIBLIOGRAPHY

Agassiz, A. 1865 North American Acalephae. Mem. Mus. Comp. Zool. 1 (2):1:234.

Agassiz, L. 1849 Contributions to the Natural History of the - Acalephae of North America. Part 1. On the naked-eyed Medusae of the shores of Massachusetts in their perfect state of development. Mem.Amer. Acad. Arts Sci. Boston, 4,9 :221-316.

Ahlstrom, E.H. 1966 Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951-1964. A summary. U.S. Fish Wildl. Service, - Spec. Sci. Repts, Fish, 534:1-71.

Akesson, B. 1962 The Embryology of *Tomopteris helgolandica*. Acta Zool. 43:135-200.

Ali Khan J. and G. Hempel 1974 Relation of fish larvae and zooplankton biomass in the Gulf of Aden. Mer. Biol. 28:311-316.

Almeida Pradp. M. S. 1968 Distribution and annual occurrence of Chaetognatha off Cananeia and Santos coast (Sao Paulo, Brazil). Bol. Inst. Ocean. Sao Paulo, 17(1):33-55.

Alvariño, A. 1956a Zooplankton from the VENDAVAL cruise in Newfoundland waters, March, April and May 1953 (Zooplancton del crucero VENDAVAL en aguas de Terranova, durante Marzo, Abril y Mayo de 1953) Bol. Inst. Español Oceanogr. (76):1-28.

__________ 1956b Zooplankton from Newfoundland waters, March, June 1955 (Zooplancton de Terranova, Marzo, Junio 1955). Bol. Inst. Español Oceanogr. (77): 1-18.

__________ 1962 Two new Pacific Chaetognatha; their distribution and relationship to allied species. Bull. Scripps Inst. Oceanogr. Univ. California 8(1): 1-50.

____________ 1965 Chaetognatha. Oceanography and Marine Biology: Annual Review. H. Barnes, Editor; George Allen & Unwing Ltd., London Publishers, 3:115-194.

____________ 1972 A second record of a rare Siphonophore *Epibulia ritteriana* Haeckel 1888. U.S. Fish Bull, 70(2):507-509.

____________ 1974 Chaetognatha. 15th Edition of Encyclopaedia Britannica,:18-19.

____________ 1976a Predation in Coelenterates: Siphonophorae and Chondrophorae. Abstracts III Symp. Biol. Colenterates, May 1976, Victoria, British Columbia, Canada.

____________ 1976b Zooplankton and Fisheries; the role of Predation (El zooplancton y las Pesquerías; el efecto de la Depredación). I Symp. Massive Fisheries, México, Sept. 1976, pp. 277-293.

____________ 1977 Predation in the plankton realm and Fisheries (Depredadores plantónicos y la Pesca). Mem. II Latin-Amer. Symp. Biol. Ocean. Cumana, Venezuela, 1:139-160.

____________ 1978 *Spadella gaetanoi* a new benthic Chaetognatha from Hawaii. Proc. Biol. Soc. Washington, 91 (3):650-657.

____________ 1979 The relation between the distribution of zooplankton predators and *Engraulis mordax* larvae. Proc. Symp. Early Life Hist. Fish. ICES, Woods Hole, April 1979. Rapp. Proc.-Verb. Raun. Cons. Int. Explor. Mer, 178:197-199, 1981.

____________ 1980a Reproduction seasons and day/night bathymetric distribution of three species of Diphyinae (Siphonophorae), off California and Baja California. IV Intern. Symp. Coelenterates. Developmental and Cellular Biology of Coelenterates. P. Tardent and R. Tardent, Editors, pp. 33-38.

____________ 1980b The relation between the distribution of zoo plankton predators and anchovy larvae. Calif. Coop. Ocean. Fish. Invest. Rept. 21:150-160.

Ambler, J.W. and B.W. Frost 1974 The feeding behavior of a predatory planktonic copepod *Tortanus discaudatus*. Limn. Ocean. 19:446-451.

Angel, M.V. 1970 Observations on behaviour of *Conchoecia spinirostris*. Journ. Mar. Biol. Assoc. U.K. 50:731-736.

__________ 1972 Planktonic oceanic Ostracods. Historical present and future. Proc. Royal Soc. Edinburgh (B), 73(22):213-228.

Arai, M.N. 1980 Growth rates of *Aequorea* Medusae. Development and Cellular Biology of Coelenterates. P. Tardent and R. Tardent. Editors. pp. 163-169.

_______ and J. Riger Jacobs 1980 Interspecific predation of common Strait of Georgia planktonic Coelenterates: Laboratory evidence. Canadian Journ. Fish and Aquatic Sci. 37(1):120-123.

Arai, M.N. and D.E. Hay 1982 Predation by Medusae on Pacific Herring (*Clupea harengus pallasi*) larvae. Canadian Journ. Fish. and Aquatic Sci. 39(11):1537-1540.

Bailey, K.M. and R.S. Batty 1983 A laboratory study of predation by *Aurelia aurita* on larval herring (Clupea harengus): Experimental observations compared with model prediction. Mar. Biol. 72(3): 295-301.

Bailey, K.M. and J. Yen 1983 Predation by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of Pacific hake Merluccius productus. Jorn. Plankton Research, 5(1):71-82.

Bainbridge, V. and D.C.T. Forsyth 1972 An ecological survey of a Scottish Herring fishery. Part V. The plankton of the North-western North Sea in relation to the physical environment and the distribution of the herring. Bull. Mar. Ecol., 8:21-52.

Baker, L.D. and M.R. Reeve 1974 Laboratory culture of the Lobate Ctenophore *Mnemiopsis maccradyi* with notes on feeding and fecundity. Mar. Biol., 26:57-62.

Bal, D.V. and L.B. Pradhan 1952 Records of zooplankton in Bombay waters during 1944-47. Bombay University Journal, 20(5):75-79.

Baranenkova, A.S. 1961 The results of surveys on young cod and haddock in the Barentz Sea during the period 1949-1959. UNIRO, and PINRO Soviet Fish. Invest. North European Sea, pp. 267-275 (Transl. Lowestoff Fish. Lab.).

Barham, E.G. 1963 Siphonophores and the Deep scattering layer. Science, 140 (3568):826-828.

__________ 1966 Deep scattering layer migration and composition: Observations from a diving saucer. Science, 151 (3716):1399-1403.

Barnes, J.H. 1966 Studies on three venomous Cubomedusae. IN: The Cnidaria and their evolution, Editor: W.J. Rees. Symp. Zool. Soc. London, 16:305-332.

Bartels, C.O. 1910 Auf Fischer Tatbeobachtungen aus der niederen tierwelt in bilderserien nach-natur-nufnahmen. Part 1. Stuggart, pp. 1-35.

Barth, R. 1963 Estudos sobre o contenido intestinal de alguns Copepoda e Chaetognatha. Inst. de Pesq. da Marinha. Ministerio de Marinha, Brazil, 6/63: 1-18.

Beebe, W. 1928 Beneath Tropic Seas, pp. 1-234

______ and J. Tee-Van 1928 Fishes of Port-au Prince Bay, Haiti. Zoologica, 10 (1):1-279.

Berger, E.W. 1900 Physiology and Histology of the Cubomedusae, including Dr. F.S. Conant's notes on the Physiology. Mem. Biol. Lab. John Hopkins Univ. 4(4):1-84.

Berrill, N.J. 1930 On the occurrence and habits of the Siphonophore *Stephanomia bijuga* (Delle Chiaje).

Journ. Mar. Biol. Assoc. U.K., 16(3):753-755.

Bieri, R. 1961 Post-larval food of the pelagic Coelenterate *Velella lata*. Pac. Sci. 15:553-556.

_________ 1970 The food of *Porpita* and niche separation in three neuston coelenterates. Publ. Seto Mar. Biol. Lab., 17(5):305-307.

Bigelow, H.B. 1909 Coelenterates from Labrador and Newfoundland Proc. U.S. Nat. Mus., 37-301-319.

__________ 1915 Exploration of the coast water between Nova Scotia and Chesapeake Bay, July and August 1913, by the United States Schooner GRAMPUS. Oceanography and Plankton. Bull. Mus. Comp. Zool. Harvard College, 59(4):149-359.

__________ 1926 Plankton of the offshore waters of the Gulf of Maine. Bull. Bur. Fish. 40(2):Doc. 968:1-509.

Bigelow H.B. and M. Leslie 1930 Reconnaisance of the waters and plankton of Monterey, May, July 1928. Bull. Mus. Comp. Zool. Harvard, 70:429-581.

Bigelow, R.P. 1891 Notes on the physiology of *Caravella maxima* Haeckel (*Physalia caravella* Eschscholtz). Johns Hopkins Univ. Circ.10:90-93.

Biggs, D.C. 1976 Nutritional ecology of *Agalma okeni* (Siphonophora:Physonectae) Coelenterate Ecology and Behavior, G.O. Mackie editor, pp. 201-210.

__________ 1977 Field studies of fishing, Feeding and digestion in Siphonophore Mar. Behav. Physiol. 4(4):261-274.

______ and G.R. Harbison 1976 The Siphonophore *Bathyphysa sibogae* Lens and van Riemsdijk 1908 in the Sargasso Sea, with notes on its natural history. Bull. Mar. Sci. 26(1):14-18.

Bishop, J.W. 1967 Feeding rates of the Ctenophora *Mnemiopsis leidyi*. Chesapeake Sci., 8:259-261.

___________ 1968 A comparative study of feeding rates of tentaculate Ctenophores Ecol. 49:996-997.

Blaxter, J.H.S. and G. Hempel 1963 The influence of egg size on herring larvae *Clupea harengus*). Journ. Cons. Int. Explor. Mer. 28:211-240.

Brooks, E.R. 1970 Selective feeding of some adult female copepods on an array of food including *Artemia* and naturally-occurring nauplii. Inst. Mar. Resources, Res. Mar. Food Chain Prog. Rept. July 1969 June 1970, 1:57-74.

Browne, E.T. 1900 The Fauna and flora of Valencia Harbor on the west coast of Ireland. The pelagic fauna (1895-98). II The Medusae, (1895-98). Proc. R. Ir. Acad. 3rd Sci., 5(5):667-736.

Burrell, V.G. and W.A. van Engel 1976 Predation and distribution of a Ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River Estuary. Estuarine and Coastal Mar. Sci., 4:235-242.

Burukovskyi, R.N. and Yu. M. Froyerman 1973 An approach to the study of hunting by predatory marine Invertebrates. Oceanology, 14(1):133-137.

Candeias, A. 1931 Contribucao para o conhecimento dos Coelenterados planctonicos das costas portuguesas. Mem. & Estudos Museo Zool. Coimbra Univ. Ser. 1(57): 5-11.

Cargo, D.G. 1975 Comments on the laboratory culture of Scyphczoa. Culture of Marine Invertebrate Animals, pp. 145-154.

__________ and L.P. Schultz 1966 Notes on the biology of the Sea nettle *Chrysaora quinquecirrha*, in Chesapeake Bay. Chesapeake Sci., 7(2):95-100.

__________ 1967 Further observations on the biology of the Sea nettle *Chrysaora quinquecirrha* and jelly fishes in Chesapeake Bay. Chesapeake Sci., 8(4):209-220.

Chun, C. 1880 Die Ctenophores des Golfes von Neapel und der eugrenzeuden Meeresabschnitte. Fauna und Flora des Golfes von Neapel I Monogr. XVIII+313 pages.

Ciechmoski, J.D.Z. de 1966 Development of the larvae and variations in the size of the eggs of the Argentine anchovy *Engraulis anchoita* Hubbs and Marini. Journ. Cons. Intern. Explor. Mer, 30:281-290.

Clarke, M.R. and P.J. Herring 1969 Animal miscellany: As survey of Oceanic Families. IN: Deep Oceans, P.J. Harring and M.R. Clarke, Editors, pp. 164-204.

Conant, F.S., 1897 Notes on the Cubomedusae. Mem. Biol. Lab. Johns Hopkins Univ. 17:8-10.

Conover, R.J. 1960 The feeding behavior and respiration of some marine planktonic crustacea. Biol. Bull, Woods Hole, 119:399-415.

Corbin, P.G. 1947 The spawning of mackerel *Scomber scombrus* L. and pilchard *Clupea pilchardus* Walbaum in the Celtic Sea in 1937-39. Journ. Mar. Biol. Assoc. U.K. 27:65-122.

Cort Basilio, J.L. and G. Pérez-Gandaras Pedrosa 1973 Estudios de pesca de los Cefalópodos (*Octopus vulgaris*, *Sepia officinalis hierredda y Loligo vulgaris*) del banco pesquero Sahariano. Bol. Inst. Español Oceanogr. (173):1-63.

Cosper, T.C. and M.R. Reeve 1975 Digestive efficiency of the Chaetognath *Sagitta hispida* Conant. Journ. Exp. Mar. Biol. Ecol. 17:33-38

Dahl, E. 1961 The association between young whiting, *Gadus merlangus* and the jellyfish *Cyanea capillata*. Sarsia (3):47-55.

Damas, D. 1909a Review of Norwegian fishery and marine investigations 1900-1908. Plankton Rep. Norw. Fish. Mar. Invest. 2(1):93-107.

________ 1909b Contribution à la biology des Gadides. Rapp et Proc-Verb. Réun. Cons. Perm. Intern. Explor. Mer, 10(3):1-277.

Dantan, J.L. 1925 Contribution à l'Estude du *Tetraplatia volitans* Annals Inst. Oceanogr. Monaco, n.s. 2:429-359.

David, P.M. 1955 The distribution of *Sagitta gazellae* Ritter-Zahony. Discovery Reports, 27:235-278.

Dekhnik, T.V., L.A. Duka and V.I. Sinyukova 1970 Food supply and the causes of mortality among the larvae of some common Black Sea fishes. Prob. Ichthyol. 10:304-310.

Delap, M.J. 1901 Notes on the rearing of *Chrysaora isosceles* in an aquarium. Ir. Nat. 10:25-28.

___________ 1905 Notes on the rearing in an aquarium of *Cyanea lamarcki* Péron & Lésueur. Rep. Sea Inld Fish. Ire. (1902-03)2, Sci. Invest. pp:20-22.

___________ 1907 Notes on the rearing in an aquarium of *Aurelia aurita* L. and *Pelagia perla* (Slabber). Rep. Sea Inld, Fish. Ire (1905). 2 Sci. Invest. pp. 160-164.

Della Croce, N. 1963 Osservazioni sull'alimentazione di *Sagitta*. Int. Comm. Sci. Explor. Mer Méditerranée. Rapp. Proc. Verb. Réun. 17(1):627-63.

Devold, F. 1935 The susceptibility of plaice eggs to shock. K. norske Vidensk, Selsk. Forh. 8:71-74.

Dollfus, R.P. 1963 List. of Palearctic and Indian Sea Coelenterate where have been found some digenetic Trematoda. Bull. Inst. Pêche Marit. Maroc. (9-10): 33-57.

Drzewina, A. and G. Bohn 1911 Modifications rapides de la forme sous l'influence de la privation d'oxygen chez una meduse, *Eleutheria dichotoma* Quatrefages. C.R. Acad. Sci. Paris, 153, p. 1030.

___________ 1912 Observation sur l'*Eleutheria claparedei* Hart et son polype. C.R. Soc. Biol. Paris, 63:p 393.

___________ 1913 Observations biologiques sur *Eleutheria dichotoma* Quatrefages et *E. claparedei* Hart. Arch. Zool. Exp. Gen. Paris, 53:15-59

Duvault, Y. 1965 A propos de la "feeding reaction" chez deux Siphonophores Calycophorides. Bull. Inst. Ocean.

Alger, Pelagos, 2(3):45-54.

Eakin, R.M. and J.A. Westfall 1964 Fine structure of the eye of a chaetognath. The Journ. of Cell Biology, 21(1):115-132.

Elian, L. 1960 Observations systematiques et biologiques sur les Chaetognathe qui se trouvent dans les eaux Roumaines de la Mer Noire. Rapp. Proc. Verb. Réun. Comm. Intern. Explor. Mer Méditerranée 15(2):359-366.

Elofson, O. 1941 Zur Kenntnis des marinen Ostracoden Schwedens, mit besenderer berückschtigung des Skageraks. Zool. Bidr. Uppsala, 19:215-51

Enomoto, Y. 1956 On the occurrence and the food of *Noctiluca scintillans* (Macartney) in the waters adjacent to the west coast of Kyushu, with special reference to the possibility of the damage caused to the fish eggs by that plankton. Bull. Japanese Soc. Sci. fish. 22(2):82-88.

Esterly, C.D. 1916 The feeding habits of pelagic Copepods. Univ. California Publ. in Zool. 16(14):171-184.

Fabricius, O. 1780 Fauna Groenlandica, pp XVI, 1-452.

Filipova, Yu. A. 1974 On the food habits of the oceanic squids of the family Ommastrephidae. IN: Distribution and biology of Commercial Invertebrates and algae. Moissev, Editor. 5:123-132.

Fish, C.J. and M.C. Cobb 1954 Noxious marine animals of the Central and Western Pacific Ocean. Res. Rep. U.S. Fish. Serv. (36):1-45.

Fisher, L.R. and E.H. Goldie 1959 The food of *Meganyctiphanes norvegica* (M. Sars) with an assessment of the contributions of its components to the vitamin A reserves of the animal. Journ. Mar. Biol. Assoc. U.K., 38:291-312.

Fraser, J.H. 1952 The Chaetognatha and other zooplankton of the Scottish area and their value as biological indicators of Hydrographical conditions. Mar.

Res. Scot. (2):1-52.

Fraser, J.H. 1961 The oceanic and bathypelagic plankton of the North-East Atlantic and its possible significance to fisheries. Mer.Res. Scot. (4):1-48.

__________ 1962 The role of Ctenophores and Salps in zooplankton production and standing crop. Rapp. and Proc.-Verb. Réun. Cons. Perm. Intern. Explor. Mer. 153(19):121-123.

__________ 1969 Experimental feeding of some Medusae and Chaetognatha, Journ. Fish. Res. Bd. Canada, 26(7): 1743-1762.

__________ 1970 The ecology of the Ctenophore *Pleurobrachia pileus* in Scottish waters. Journ. Cons. Intern. Explor. Mer, 33:149-168.

Fukuchi, M., Y. Yoshida and A. Hara 1971 An observation on feeding behavior of macrozooplankton. Bull Plankt. Soc. Japan, 18(2):62-64.

Fulton, R.S. 1982 Predatory feeding of two marine mysids. Mar. Biol. 72(2):183-191.

Furnestin, M.L. 1953 Chaetognathes recoltes en Méditerranée par le President Théodore-Tissier aus mois de Juin et Juillet 1950. Bull. St. Aquac. et Peche de Castiglione, N.S. (4):277-314.

__________ 1957 Chaetognathes et zooplancton du secteur Atlantique marocain. Rev. Trav. Inst. Pêches Maritimes, 21(1-2):1-356.

__________ 1959 Sur la coloration du tube digestif de certains chaetognathes. Soc. Zool. France, Paris. Bull. 84(2-3):132-135.

__________ 1960 Zooplancton du Golfe du Lion et de la cote orientale de Corse. Rev. Trav. Inst. Pêches Maritimes, 24(2):153-252.

Gaede, H.M. 1816 Beitrage sue Anatomie und Physiologie des Medusen, nebst einem Versuch einer Einteitug uber das, was den altern Naturforschern in

Hinsicht dieser Thiere bekannt was. 23 pages, Berlin.

Garstand, W.R. 1900 Preliminary experiments on the rearing of sea fish larvae. Journ. Mar. Biol. Assoc. U.K. 6:70-93.

Gladefelter, W.B. 1973 A comparative analysis of the locomotory systems of Medusoid Cnidaria. Helgolander Wiss. Meeresunters, 25:228-272.

Glover, R.S., G.A. Cooper and D.C.T. Forsyth 1961 An Ecological survey of a Scottish herring Fishery. Part III. Geographical and ecological groups in the plankton. Bull. Mar. Ecol. 5(47):195-205.

Gould, D.T. 1966 The swimming and feeding of planktonic Copepods. Some Contemporary Studies in Mar. Sci. pp. 313-334.

Graham, A. 1955 Molluscan diet. Proc. Malacol. Soc. London, 31 (3-4):1-6

Graham, M. 1943 The Fish Gate. Faber & Faber, London, 1-196.

__________, G.C. Trout, R.J.H. Beverton, J. Corlett, A.J. Lee and R.W. Blacker 1954 Report on research from Ernest Holt into the fishing near Bear Island, 1949 and 1950. Fish. Invest. London, Ser. 2, 18(3):1-87.

Grey, B.B. 1930 Chaetognatha from the Society Islands. Proc. Royal Soc. Queensland, 42(6):62-67.

Gudger, W.W. 1937 Jellyfishes as fish eaters. New York Zool. Soc. Bull. 37(2):47-58.

__________ 1942 *Physalia*, the fish-eater. Animal Kingdom Bull. New York Zool. Soc., 42(3):62-66.

__________ 1943 Some Ctenophora fish-catchers. Sci. Monthly, 57:73-76.

Gulland, J.A. 1965 Survival of the youngest stages of fish, and its relation to year-class strength. ICNAF Espec. Publc. 6B-9:363-371.

Hagmeir, A. 1933 Die Zuchtung verschiedener wirbelloser Meerestiere Abderhalden's Handbuch der biologischei Arbeitsmethoden, 9(5):465-598.

Hamann, O. 1881 Die Mundarme der Rhizostomen undihre Auhangsorgane. Jena Z. Naturw. 15:243-285.

Hamner, W.M., L.P. Madin, A.L. Alldredge, R.W. Gilmer, and P.O. Hamner 1975 Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. Limnol. & Ocean. 20(6): 907-917.

Hand, C 1955 A study of the structure affinities and distribution of *Tetraplatia volitans* Bush (Coelenterate, Hydrozoa; Pteromedusae). Pac. Sci. 9:332-348.

Harbison, G.R., L.P. Madin and N.R. Swanberg 1978 On the natural history and distribution of oceanic Ctenophores. Deep-Sea Res., 25:233-256.

Harding, G.C.H. 1974 The food of Deep-Sea Copepoda. Journ. Mar. Biol. Assoc. U.K. 54:141-155.

Harding D. and J.W. Talbot 1973 Recent studies on the eggs and larvae of the plaice (*Pleuronectes platessa* L.) in the southern bight. Rapp. Proc.-Verb Réun. Cons. Intern. Explor. Mer 164:261-269.

Hardy, A.C. 1956 The Open Sea. Collins, London, 335 pages.

Hargitt, C.W. 1902 Notes on the Coelenterate fauna of Woods Hole. Amer. Nat. 36:549-560.

———————— 1905a Medusae of the Woods Hole region. Bull. U.S. Bur. Fish. 25:23-77.

———————— 1905b Variations among Scyphomedusae. Journ. Exp. Zool. 2:547-582.

———————— and G.T. Hargitt 1910 Studies on the development of the Scyphomedusae Journ. Morphol. 21:217-262.

Hartig, J.H., J. Jude, and M.S. Evans 1982 Cyclopod predation on Lake Michigan fish larvae. Can. Journ. Fish.

Aquatic Sci. 39:1563-1568.

Hartlaub, C. 1897 Die Hydromedusen Helgolands. Wiss. Meeresuntersuch. (N.F.) 2(1)X:449-512.

Hattory, S. 1962 Predatory activity of *Noctiluca* on anchovy eggs. Bull. Tokay Reg. Fish. Res. Lab. 9:211-220.

Hela, I. 1951 On the occurrence of the jellyfish *Aurelia aurita* L. on the south coast of Finland. Sunomae Elain Karvit, Seur van Tiedon, 6:71-78.

Hempel, G. 1965 On the importance of larval survival for the population dynamics of marine food fish. Calif. Coop. Oceanic Fish. Invest. Rept. 1:13-23.

__________ and W. Weikert 1972 The neuston of the Subtropical and boreal northeastern Atlantic Ocean. A review. Mar. Biol. 13:70-88.

Hensen, V. 1887 Ueber die Bestimmung des Plankton's oder des im Meere Treibende Materials au Pflanzer und Thieren. Ber. Komm. wiss. Unters. Deutsch. Meere, Kiel. (5):1-108.

Heron, A.C. 1973 A specialized predator-prey relationship between the copepod *Sapphirina angusta* and the pelagic tunicate *Thalia democratica*. Journ. Mar. Biol. Assoc. U.K. 53-429-435.

Herrnkind, W., J. Halusky, and P. Kanciruk 1976 A further note on phyllosoma larvae associated with Medusae. Bull Mar. Sci. 26(1):110-112.

Hesthagen, I.H. 1971 On the biology of the bottom-dwelling Trachymedusa *Tesserogastria musculosa* Beyer. Norwegian Journ. Zool. 19 (1):1-19.

Heydorn, A.E.F. 1959 The Chaetognatha off the west coast of the Union South Africa. Department of Commerce and Industry, Invest. Report, (36):1-56.

Heyrand, M. 1979 Food ingestion and digestive transit time in the euphausiid *Meganyctiphanes norvegica* as a function of animal size. Journ. Plankton Res. 1(4):301-311.

Hirota, J. .1972 Laboratory culture and metabolism of the Planktonic Ctenophora *Pleurobrachia bachei* A. Agassiz. Biol. Ocean. Northern North Pacific, Editor A.Y. Takenouti, pp. 465-484.

__________ 1974 Quantitative natural history of *Pleurobrachia bachei* in La Jolla bight. U.S. Fish. Bull. 72: 295-335.

Hjort, J. and K. Dahl 1900 Fishing experiments in Norwegian fiords. Rep. Norw. Fishery Mar. Invest. 1(1): 1-215.

Hodgkin, E.P. and R.J. Rippingale 1971 Interspecies conflict in Estuarine Copepods. Limn. and Oceanogr. 16: 573-576.

Hollowday, E.D. 1974 A note on the capture of Marine Rotifera as food by Hydroid Medusae. Journ. Quekett. Micr. Club. Ser. 4,2(4):190-192 (Dec).

Holt, E.W.L. and W.M. Tattersall 1905 Biscayan plankton. Part V. Schizopoda. Trans. Linn. Soc. Zool. 10(2):103-129.

Horridge, G.A. 1965a Non-motile sensory cilia and neuromuscular functions in a ctenophore independent effector organ. Proc. Roy. Soc. London B. 162: 333-350.

__________ 1965b Macrocilia with numerous shafts from the lips of the Ctenophore *Beroë*. Proc. Royal Soc. London B. 162-351-364

__________ 1966 Some recent discovered underwater vibration receptors in invertebrates. IN: Some Contemporary Studies in Marine Science Ed. H. Barnes. Allen & Unwin, London, pp. 395-406.

__________ and P.S. Boulton 1967 Prey detection by Chaetognatha via vibration sense. Proc. Royal Soc. London, B. 168:413-419.

Hu, Vernon J.H. 1978 Relationship between vertical migration and diet in four species of euphausiids. Limn. and Oceanogr. 23(2):296-300.

Hunter, J.R. 1976 Report of a colloquium on larval fish mortality studies and their relation to Fishery Research. January 1975. NOAA Techn. Rept. NMFS Circ. 395:1-5.

__________ 1979 Feeding ecology and predation of marine fish larvae. Lectures at the University of Washington, College of Fisheries. Sea Grant Lectureships on the Early Life History of Marine Fishes, April/May, 1979.

Hunter, J.R. 1984 Inferences regarding predation on the early life stages of cod and other fishes. Flødevigen rapportser., 1:533-562. The Propagation of Cod *Gadus morhua* L.

__________, J. Taylor and E.G. Moser 1979 Effects of ultraviolet radiation on eggs and larvae of northern anchovy (*Engraulis mordax*) and Pacific mackerel (*Scomber japonicus*) during the embryonic stages. Photochemistry and Photobiology, 29: 325-338.

Huntley, M.E. and L.A. Hobson 1978 Medusa predation and plankton dynamics in a temperate Fjord, British Columbia. Fish. Res. Bd. Canada, 35 (2):257-261.

Hurley, A.C. 1976 Feeding behaviour, food consumption, growth and respiration of the Squid *Loligo opalescens* raised in the laboratory. Fish. Bull. U.S. 74: 176-182.

Hüsing, J.D. 1956 Zur Frage der Ernahrung der Ohrenqualle *Aurelia aurita* L. Scyphozoa, Semaeostomae. Wiss. Z. Martin-Luther Univ. Halle-Wittenb. (V Jahrg) 3:479-481.

Huxley, T.H. 1858 The Oceanic Hydrozoa. Ray. Soc. London, 1-141.

Hyman, L. 1940 The Invertebrates, Protozoa through Ctenophores, McGraw-Hill, N.Y., 726 pages.

Iles, E.J. 1961 The appendages of the Halocyprididae. Discovery Rept. 31:299-32.

Ishida, J. 1936 Note on the digestion of *Charybdea rastonii*. Annot, Zool. Japan. 15:449-452.

Johannes, R.E. 1978 Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3(1): 65-84.

Johnson, M.E. and H.J. Snook, 1927, 1963 Seashore animals of the Pacific coast. New York, McMillan & Co. pp. 1-659.

Johnson, M.W. 1942 Some observations on the feeding habits of the *Octopus*. Science, 95 (2471):478-479.

Jones, S. 1960 Notes on animal associations. 2 The Scyphomedusa *Acromitus flagellatus* Stiasny and young *Seleroides leptolepis* (Cuvier & Valenciennes) with the latter forming a vanguard. Journ. Mar. Biol. Assoc. India 2(1):51-52.

Joubin, L. 1924 La destruction des petits poissons par les animaux du plancton. Bull. Soc. Ocean. France, 4$^{\underline{e}}$ ann. pp.380-382.

Jumao-as, M.D.B. and H. von Westernhagen 1975 Vertical distribution of Epiplanktonic chaetognaths in the upper 100 m of the Hilutangan Chanel Cebu, the Philipines. Mar. Biol., 29:201-210.

Kamshilov, M.M. 1959 Interrelations between organisms and the part they play in evolution. Zz. Obshch. Biol. 20(5):370-378.

__________ 1960a Feeding of Ctenophore *Beroë cucumis* (Fabr.). Dokl. Akad. Nauk, 130(5):1138-1140.

__________ 1960b Biology of Ctenophores off Murman. ICES, CM, 1960 Doc. No. 157 (mimeo).

__________ E.A. Zelikman and M.I. Roukhiyainen 1958. Plankton of Murman coastal waters. IN: Collected Papers on regulations in concentration and migration of food fishes. Izd. Acad. Nauk, SSSR:59-102

Karlovac, J. 1962 Etude de l'ecologie de la sardine, *Sardina pilchardus* Walb., dans la phase planctonique de sa vie en Adriatique molenne. Acta Adriatica, 13(2):1-109.

Karpov, K.A. 1979 Prey composition of the market squid, *Loligo opalescens* Berry in relation to depth and location of capture, size of squid and sex of spawning squid. CalCOFI Rept. 20:51-57.

Kimor, B. 1979 Predation by *Noctiluca miliaris* Souriray on *Acartia tonsa* Dana eggs in the inshore waters of Southern California. Limn. Ocean. 24(3): 568-572.

Kincaid, T.B. 1915 Oyster culture in Washington. Trans. 2nd. A. Mtg. Pac. Fish. San Francisco, p.4

King, K.R. 1979 The life history and vertical distribution of the chaetognath *Sagitta elegans* in Dabob Bay, Washington. Journ. Plankton Res., 1(2):153-167.

Kotori, M. 1969 Vertical distribution of Chaetognatha in the northern North Pacific and Bering Sea. Bull. Plankton Soc. Japan 16(1):52-57.

Kramp, P.L. 1950 Freshwater Medusae in China. Proc. Zool. Soc. London, 120 (1):165-184.

__________ 1961 Synopsis of the Medusae of the World. Journ. Mar. Biol. Assoc. U.K. 40:1-469.

Kremer, P. 1979 Predation by the Ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Estuaries, 2(2):97-105.

Kuhl, W. 1932 Rippenquallen beim bentefang. Natur. Mus. Frankf. 62:130-133.

Kuhlmann, D. 1977 Laboratory studies on the feeding behaviour of the chaetognaths *Sagitta setosa* J. Müller and *S. elegans* Verrill with special reference to fish eggs and larvae as food organisms. Meeresforschung Repts. on Marine Res. Deut. Wiss. Komm. Meeresf. 25:163-171.

Lakkis, S. 1971 Contribution à l'étude du zooplancton des eaux libanaises. Mar. Biol. 11:138-148.

Lampitt, R.S. 1978 Carnivorous feeding by a small marine copepod. Limn. Ocean. 23(6):1228-1231.

Landry, M.R. 1978 Predatory feeding behavior of a marine copepod *Labidocera trispinosa*. Limn. Ocean. 23(6): 1103-1113.

__________ 1981 Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus* Mar. Biol. 65(1):77-82.

Larson, R.J. 1976 Cubomedusae feeding-Functional morphology, Behavior and philogenetic position. Coelenterate Ecology, G.O. Mackie, Editor, pages 237-245.

__________ 1980 A new Stauromedusa, *Kishinouyea corbini* (Scyphozoa, Stauromedusae) from the tropical western Atlantic. Bull. Mar. Sci. 30(1):102-107.

Lasker, R. 1965 The physiology of Pacific Sardine embryos and larvae. Calif. Coop. Ocean. Fish. Invest. Rept. 10:96-101.

__________ 1975 Field criteria for survival of anchovy larvae. The relation between inshore chlorophyll maximum layers and successful first feeding. U.S. Fish. Bull. 73(3):453-462.

Lawless, E. 1877 On a fish sheltering medusa. Nature, London 16:227.

Lazareva, L.P. 1962 On the feeding of the Black Sea Ctenophore *Pleurobrachia pileus* O.F. Müller. Trudy Karadags'ka Biol. Sr. 18:71-84.

Lebour, M.V. 1922 The food of plankton organisms, Journ. Mar. Biol. Assoc. U.K. 12:644-677.

__________ 1923 The Food of plankton organisms. II. Journ. Mar. Biol. Assoc. U.K. 13:70-92.

Lebour, M.V. 1925 Young anglers in captivity and some of their enemies. Journ. Mar. Biol. Assoc. U.K. 13:721-734.

Lebour, M.V. 1947 An interesting young *Velella* in the Plymouth plankton. Journ. Mar. Biol. Assoc. U.K. 26: 548-550.

Lee, J.Y. 1966 Oeufs et larves planctoniques de poissons. Inst. Sci. Pêches Maritimes, Spec. Publ. (3):59-96.

Lee, R.F. 1974 Lipids of zooplankton from Bute Inlet, British Columbia. Journ. Fish. Res. Bod. Canada, 31 (10):1577-1582.

Lesson, R.P. 1843 Histoire Naturelle des Zoophytes Acalephes. Paris, pp. 1-596.

Leuckart, R. 1853 Die Siphonophores. Eine zoologisch untersuchungen. Giessen pp. 1-95.

Lillelund, K. and R. Lasker 1971 Laboratory studies of predation by Marine Copepods on fish larvae. U.S. Fish. Bull. 69(3):655-667.

Linko, A. 1900 Observations sur les meduses de la Mer Blanche. Trav. Soc. Hist. Nat. St. Petersbourg, 29(4): 137-156 (1899).

Loginova, N.P. and N.M. Perzova 1967 Some data on ecology of feeding of pelagic Coelenterata of the White Sea. Issledovanilla fauni morei, 7(15):21-28.

Lonsdale, D.J., D.R. Heinle and C. Siegfried 1979 Carnivorous feeding behavior of the adult Calanoid Copepod *Acartia tonsa* Dana. Journ. Expl. Mar. Biol. Ecolog. 36(3):235-248.

Lucas, C.E. and G.T.A. Henderson 1936 Association of jellyfish and other organisms with catches of herring. Journ. Mar. Biol. Assoc. U.K. 21:293-304.

Macdonald, R. 1927 Food and habits of *Meganyctiphanes norvegica* Journ. Mar. Biol. Assoc. U.K. 14:753-784.

Mackie, G.O. 1959 The evolution of Chondrophora (Siphonophora-Disconauthae). New evidence from behavioural studies. Trans Royal Soc. Canada, ser. 3, 53: 7-20.

Mackie, G.O. and D.A. Boag 1963 Fishing, feeding and digestion in Siphonophores. Publ. Staz. Zool. Napoli, 33:178-196.

Maigret, J. 1976 Contribution à l'étude des Langoustes de la côte occidentale d'Afrique (Crustaces, Decapodes, *Palinuridae*). I Notes sur la biologie et l'écologie des especies sur les côtes du Sahara. Bull. Inst. Fondamental d'Afrique Noire, Bull. Ser. Sci. Naturelles, 38(2):266-302.

Main, R.J. 1928 Observations on the feeding mechanism of a Ctenophore, *Mnemiopsis leidyi*. Biol. Bull. Woods Hole, 55(2):69-78.

Mansueti, R. 1963 Symbiotic behavior between small fishes and jellyfishes, with new data on that between the Stromateid, *Peprilus alepidotus* and the Scyphomedusa *Chrysaora quinquecirrha*. Copeia 1963 (1):40-78.

Mantenfel, B.P. 1941 Plankton and herring in the Barents Sea, Trudy Polyar. nachnoissled Instn. Morsk. Ryb. Khoz, Okeanogr. 7:125-218.

Marinaro, J.Y. and M. Bernard 1966 Contribution à l'étude des oeufs et larves pélatiques de poissons méditerranéens. Note preliminaire sur l'influence léthale du rayonnement solaire sur les oeufs. Pelagos, 7:48-55.

Massuti Oliver, M. 1954 Sobre la biología de las *Saggittas* del plancton del Levante Español. Inst. Biol. Apl., 16:137-148.

Matthews, J.E. and H.H. Shoemaker 1952 Fishes using Ctenophores for shelter. Copeia, 1952 (4):270.

Mauchline, J. 1970 The biology of *Mysidopsis gibbosa, M. didelphis and M. angusta* (Crustacea, Mysidacea). Journ. Mar. Biol. Assoc. U.K. 50:381-396.

May, R.C. 1974 Larval mortality in Marine Fishes and the critical period concept. IN: Early life History of fish. Proc. Internl Symp. pp. 3-19.

Mayer, A.G. 1898 Studies from the New Port Marine Laboratory on *Dactylometra*. Bull. Mus. Comp. Zool. Harvard College, 32(1):1-11.

——— 1910 The Medusae of the World. Vols. 1, 11, 111, pages 1-735.

——— 1912 Ctenophores of the Atlantic coast of North America. Publ. Carnegie Instn. (162):1-58.

——— 1917 Report upon the Scyphomedusae collected by the U.S. Bureau of Fisheries Steamer ALBATROSS in the Philippine Islands and Malay Archipelago. U.S. Nat. Mus. Bull. (100):175-233.

McCrady, J. 1858 *Gymnophthalmata* of Charleston Harbor. Proc. Elliot Soc. Nat. Hist. Charleston, South Carolina, 1:103-294.

McIntosh, W.C. 1926 Additions to the Marine fauna of St. Andrews since 1874. Ann. Mag. Nat. Hist. Ser. 9, 18:241-266.

McLaren, I.A. 1966 Adaptative significance of large size and long life of the chaetognath *Sagitta elegans* in the Arctic. Ecology, 47(5):852-855.

McNamara, P. 1955 Sea Nettles observed to feed on sea walnutts in Laboratory. Maryland Tidewater News, 12(6): 3.

Mikhailov, B.N. 1962 On the feeding of the Black Sea Medusae *Aurelia aurita*. Zoologichskii Zhurnal, 41(2): 286-287.

Miller, R.J. 1974 Distribution and biomass of an estuarine Ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). Chesapeake Sci., 15(1):1-8.

Mills, C. and J. T. Rees 1979 *Bythoriara stilbosa*, new species (Anthomedusae: Calycopsidae) from neritic waters in Central California. Journ. Natural History, 13:285-293.

——— and C. Hand 1976 A new species of *Aglauropsis* (Hydrozoa; Limnomedusae) from the Northeastern Pa cific, with notes on *Aglauropsis conantii* and *Eperetmus typus*. The Wasmann Journ. Biol. 34 (1):23-42

Mironov, C.N. 1960 The food of plankton predators. II Food of *Sagitta*. Trud. Sebastopol Biol. Stat., 13:78-80.

Moeller, H. 1979 Jellyfish are also strongly fishing (Quallen fischen Kradftig mit). Fisherblatt, 27(9):249-253.

Moeller, H. 1982 Effect of Jelly fish predation on larval herring in Kiel Bight. Coun. Meet. Int. Counc. Explor. Sea 1982. Colleted papers (3:11):1-8.

Moeller, H. 1983 Die Bedentung der Quallen fuer das planktonsystem der Kieler Bucht. Inst. Meereskd. Univ. Kiel. Collect. Rept. Inst. Meereskd. Univ. Kiel Vol. 1981. Summary only.

Möller, H.N. 1979 Significance of coelenterates in relation to other plankton organisms. Meeresforschung Repts. Mar. Biol. Deutschen Wiss. Komm. Meeresforschung 27(1):703-712.

______________ 1980 Scyphomedusae as predators and food competitors of larval fish. Meeresforschung Repts. Mar. Res.Besicht Deutsch. Wiss. Komm. Meeresforschung, 28(2-3):90-100.

Murakami, A. 1959 Marine Biological Study on the planktonic chaetognaths in the Seto Inland Sea. Bull. Naikai Regional Fish. Res. Lab., Ujina, Japan, 12:1-186.

Murphy, G.I. 1961 Oceanography and variation in the Pacific Sardine population Calif. Coop. Oceanic Fish. Invest. Rept. 8:55-64.

Murray, J. and J. Hjort 1912 The Depths of the Ocean. pp. 1-821.

Nagabushanam, A.K. 1959 Feeding of a Ctenophora, *Bolinopsis infundibulum* (O. F. Mülle Nature, London, 184:829.

Nagabushanam, A.K. and J.T. Jothinayagam 1977 Observations on the rearing of young Ctenophores, *Pleurobrachia globosa* Moser 1903 (Class: Tentaculata; Order: Cydippida) in marine aquaria. IN: Proc. Symp. Warm Water Zooplankton, Goa, India, NIO, India, pp. 379-382.

Nagasawa, S. and R. Marumo 1972 Feeding of a pelagic Chaetognatha *Sagitta nagae* Alvariño in Suruga Bay, Central Japan. Journ. of Ocean. Soc. Japan, 28(5): 181-186.

____________ 1976 Further studies on the feeding habits of *Sagitta nagae* Alvariño in Suruga Bay, Central Japan. Journ. Ocean. Soc. Japan, 32:209-218.

Nair, K.K. 1947 Medusae of Travancore and their correlation with inshore fishing. Proc. Indian Sci. Congress Assoc., Calcutta, 32(3):97.

Nair, V.R. 1976 Studies on Predation on fish eggs and larvae by chaetognaths. Special Publ. Proc. Symp. Warm Water Zooplankton, India, pp. 425-431.

________ and T.S.S. Rao 1973 Chaetognaths of the Arabian Sea. Ecological Studies, Analysis and synthesis, 3: 293-544 (Ed. Zeitzschel).

Neale, I.M. and I.A.E. Bayly 1974 Studies on the Ecology of the zooplankton of four estuaries in Victoria. Australia Journ. Mar. Freshwat. Res., 25:337- 350.

Neis, K.N. 1977 Population structure of the squid *Sthenoteuthis onalaniensis* (Lesson 1830) (Ommastrephidae) in the tropical western Pacific. Academy of Sciences USSR (Akad. NAUK SSSR), 107 (13):15-27. Transl. NMFS, U.S. Depart. Commerce, Office of International Fisheries.

Nelson, T.C. 1925 On the occurrence and food habits of ctenophores in New Jersey inland waters. Biol. Bull. 48:92-111.

Nemoto, T. 1972 Chlorophyll pigments in the stomach and gut of some macrozooplankton species. Biol. Ocean.

Northern North Pacific, Edit. A.Y. Takenouti, pp. 212-218.

________ 1977 Food and feeding structures of Deep-Sea *Thysanopoda* Euphausiids. Oceanic Sound Scattering Prediction, pp. 457-480.

________ and Kwand II Yoo 1970 An Amphipod *Parathemisto gaudichaudii* as a food of the Antarctic Sei Whale. Sci. Rept. Whales Res. Inst. (22):153-158.

Newbury, T.K. 1972 Vibration perception by Chaetognaths. Nature, 236(5348):459-460.

________ 1978 Consumption and growth rates of chaetognaths and copepods in Subtropical Oceanic waters. Pac. Sci. 32(1):61-78.

Nicol. J.A. Colin 1960 Biology of Marine Animals, pp. 1-707.

Novotny, A.J. and C.V.W. Mahnken 1971 Predation on juvenile Pacific Salmon by a marine Isopod *Rocinela belliceps pugettensis* (Crustacea, Isopoda). Fish Bull, U.S. 69(3):699-701.

Oesterbol, A. 1885 Fish and Medusae. Bull U.S. Fish Comm. 5: 331-332.

Okutani, T. 1961 Notes on the genus *Carinaria* (Heteropoda) from Japanesa and adjacent waters. Publ. Seto Mar. Biol. Lab. 9(2):333-352.

Omori, M. 1969 The biology of a Sergestid schrimp *Sergestes lucens* Hansen. Bull. Ocean. Res. Inst. Univ. Tokyo, (4):1-83.

Orton, J.H. 1922 The mode of feeding of the jelly-fish *Aurelia aurita*, on the smaller organisms in the plankton. Nature, London, 110(2753):178-179.

Oye, P. van 1918 Untersuchungen uber die Chaetognathe des Javameeres. Contrib. à la Fauna des Indes Neerlandaises, 4:1-61.

Parry, D.A. 1944 Structure and fuction of the gut in *Spadella* *cephaloptera* and *Sagitta setosa*. Journ. Mar. Biol. Assoc. U.K. 26 (1):16-36.

Pearre, S. 1973 Vertical migration and feeding in *Sagitta elegans* Verril. Ecology, 54:300-314.

____________ 1974 Ecological studies of three West-Mediterranean Chaetognaths. Invest. Pesq. 38(2):325-369.

____________ 1976 A seasonal study of the diets of three sympatric chaetognaths. Invest. Pesq. 40(1):1-16.

____________ 1981 Feeding by Chaetognatha: Energy balance and importance of various components of the diet of *Sagitta elegans*. Mar. Ecol. Progress Ser. 5:45-54.

Phillips, P.J. 1971 The Pelagic Cnidaria of the Gulf of México: Zoogeography, Ecology and Systematics. Ph. D. Dissertation Thesis, Texas A & M Univ., pp.-1-212.

____________ W.D. Burke and E.J. Keener 1969 Observations on the trophic significance of jelly fishes in the Mississippi sound with quantitative data on the associate behavior of small fishes with Medusae. Trans. Amer. Fish. Soc., (4):703-712.

Phillips, P.J. and W.D. Burke 1970 The occurrence of Sea Wasps (Cubomedusae) in Mississippi Sound and the northern Gulf of Mexico. Bull Mar. Sci., 20 (4):853-859.

Pommeranz, T. 1974 Resistance of Plaice Eggs to Mechanical stress and light. IN: Early Life History of Fish. Proc. Symp. Oban. Blaxter, Edit. pp. 397-416.

Poulsen, E.M. 1944 On the fluctuations in the size of the stock of cod in the waters within the Skaw during recent years. Rept. Danish Biol. Stat., 46(194): 1-36.

Purcell, J.E. 1980 Influence of Siphonophore behavior upon their natural diets: Evidence of aggresive mimicry. Science, Washington, 209 (4460):1045-1047.

___________ 1981a Feeding ecology of *Rhizophysa eysenhardti*, a Siphonophore predator of fish larvae. Limn. Ocean. 26(3):434-432.

___________ 1981b Selective predation and caloric consumption by the Siphonophore *Rosacea cymbiformis* in Nature. Mar. Biol. 63:283-294.

___________ and P. Kremer 1983 Feeding and metabolism of the Siphonophore *Sphaeronectes gracilis*. Journ. Plankton Res. 5(1):95-106.

Quatrefages, A. de 1854 Memoire sur l'organisation des physalies (Physalia). Ann. Sci. Nat. Zool. Ser. 4, 2:107-142.

Rakuza-Suszczewski, S.J. 1968 Predation of Chaetognatha by *Tomopteris helgolandica* Greff. Conseil Perm. Intern. Explor. Mer, 32:226-231.

_____ _________ 1969 The food and feeding habits of Chaetognatha in the seas around the British Isles. Polskie Archivum Hydrobiol. 16:213-232.

Ralph, P.M. and C. Kaberry 1959 New Zealand Coelenterates. Ctenophores from Cook Strait. Zool. Publs. Vict., Univ. Coll.(3):1-11.

Rao, T.S.S. 1962 Studies on Chaetognatha of the Indian Seas. Proc. First All-India Congress of Zool. The Zool. Soc. India, (2):370-375.

Rees, J.T. 1969 The polyp and immature medusa stages of *Cladonema californicum* Hayman 1947 (Anthomedusae: Cladonemidae) with biological notes and a discussion of the taxonomy of the genus *Cladonema*. Journ. Natural History, 13:295-302.

___________ 1977 Polyp and Medusa of *Dipurema bicircella* n. sp. (Hydrozoa: Corynidae) from Northern California. Mar. Biol. 39:197-202.

Rees, J.T. 1979 Growth stages of the medusa of *Proboscidactyla flavicirrata* Brandt 1836 (Hydrozoa: Limnomedusae). Canadian Journ. Zool. 57(3):551-557.

Rees, W.J. 1966 *Cyanea lamarcki* Peron & Lésueur (Scyphozoa) and its association with young *Gadus merlangus* L. (Pisces). Ann. Mag. Nat. Hist. Ser. 13, 9:285-287.

Reeve, M.R. 1964 Feeding of zooplankton with special reference to some experiments with *Sagitta*. Nature, London, 201(4915):211-213.

__________ and M.A. Walter 1972 Conditions of culture, food-size selection and the effects of temperature and salinity on growth rate and generation time in *Sagitta hispida* Conant. Journ. Exp. Mar. Biol. Ecol. 9:191-200.

__________ T.C. Cosper and M.A. Walter 1975 Visual observations on the process of digestion and the production of faecal pellets in the Chaetognatha *Sagitta hispida* Conant. Journ. Expr. Mar. Biol. Ecol. 17:39-46.

Regner, S. 1980 On some Zooplankton predators on plankton fish stages. Inst. za Oceanogr. I Ribarstvo, Split (Yugoslavia), 39, 6 pages.

Renfro, W.C. and W.G. Pearcy 1966 Food and feeding apparatus of two pelagic shrimps Journ. Fish. Res. Bd. Canada, 23:1971-1975.

Ries, J.V. and M.V. Ries 1924 Farbe und Warme. Eine licht-biologische Studie. Umschau (28 Jahrg.):666-670.

Riley, G.A. and D.F. Bumpus 1946 Phytoplankton-zooplankton relationships on Georges Bank. Journ. Mar. Res. 6:33-47.

Rippindale, R.J. and E.P. Hodgkin 1974 Predation effects on the distribution of a Copepoda. Austral. Journ. Mar. Freshwater Res. 25:81-91.

Roger, C. 1973 Recherches sur la situation trophique d'un groupe d'organismes pélagiques (Euphausiacea). I Niveaux trophiques des especes. Mar. Biol. 18: 312-316.

Rogers, C.A., D.C. Biggs and R.A. Cooper 1978 Aggregation of the Siphonophore *Nanomia cara* in the Gulf of Maine. Observations from a submersible. U.S. Fish. Bull., 76(1):281-284.

Rollefsen, G. 1930 Observations on cod eggs. Rapp. Proc. Verb. Réun. Cons. Perm. Intern. Explor. Mer, 65:31-34.

______________ 1932 The susceptibility of cod-eggs to external influences. Journ. Cons. Perm. Intern. Explor. Mer, 7:365-373.

Romanes, G.J. 1877a The fish-sheltering medusa. Nature, London, 16:248.

______________ 1877b Further observations on the locomotor System of Medusae. Phil. Trans Roy. Soc. London, 167:659-751.

Rozanska, Z. 1971 Studia nad Biologia i Ekologia Chaetognatha w Baltyku. Wyzsza Szkola Rolnicza W. Olsztynie, pp. 1-88.

Russell, F.S. 1925 The vertical distribution of Marine Macroplankton. An observation on diurnal changes. Journ. Mar. Biol. Assoc. U.K., 13:769-809.

______________ 1928 The vertical distribution of marine macroplankton. VIII Further observation on the diurnal behaviour of the pelagic young teleostean fishes in the Plymouth Area. Journ. Mar. Biol. Assoc. U.K., 15:829-850.

______________ 1930a The vertical distribution of marine macroplankton. IX The distribution of the pelagic young teleostean fishes in the daytime in the Plymouth area. Journ. Mar. Biol. Assoc. U.K. 16: 639-676.

______________ 1930b The seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the Ring-trawl in offshore waters in the Plymouth area. Journ. Mar. Biol. Assoc. U.K. 16(3):707-722.

Russell, F.S. 1931 The study of copepods as a factor in oceanic economy. 5th Pac. Sci. Congress, pp. 2023-2034.

______________ 1933 The seasonal distribution of macroplankton as shown by catches in the 2-metre stramin Ring-trawl in the offshore waters off Plymouth. Journ. Mar. Biol. Assoc. U.K., 19:73-81.

______________ 1934 The zooplankton. III A comparison of the abundance of zooplankton in the Barrier Reef Lagoon with that of some regions in the northern European waters. Sci. Rept. Great Barrier Reef Expd., 2:176-201.

Russell, F.S. 1935a The seasonal abundance and distribution of the pelagic young of Teleostean fishes caught in the Ring-trawl in offshore waters in the Plymouth area. Journ. Mar. Biol. Assoc. U.K. 20(2):147-179.

______________ 1935b On the value of certain plankton animals indicators of water movements in the English Channel and North Sea. Journ. Mar. Biol. Assoc. U.K., 20(2):309-332.

______________ 1936 The seasonal abundance of the pelagic young of Teleostean fishes in the Plymouth area. Part III. The year 1935, with a note on the conditions as shown by the occurrence of plankton indicators. Journ. Mar. Biol. Assoc. U.K. 20(3):595-604.

______________ 1938 The Plymouth offshore Medusa Fauna. Journ. Mar. Biol. Assoc. U.K., 22:411-440.

______________ 1939 Hydrografical and biological conditions in the North Sea as indicated by plankton organisms. Journ. du Conseil Intern. Explor. Mer. 14(2):171-192.

Russell, F.S. 1952 The relation of plankton research to Fisheries Hydrography. Rapp. et Proc. Verb. Cons. Intern. Explor. Mer, 131:28-34.

____________ 1953 The Medusae of the British Isles. Cambridge Press, pp. 1-530.

____________ 1970 The Medusae of the British Isles. Part II Cambridge Press, pp. 1-284.

_________ and W.J. Rees 1936 On rearing the hydroid *Zanclea implexa* (Alder) and its medusa *Zanclea gemmosa* McCrady, with a review of the genus *Zanclea*. Journ. Mar. Biol. Assoc. U.K. , 21:107-129.

Sameoto, D.D. 1972 Yearly respiration rate and estimated energy budget for *Sagitta elegans*. Journ. Fish. Res. Bd. Canada, 29(7):987-996.

____________ 1975 Tidal and diurnal effects on zooplankton sample variability in a nearshore Marine environment. Journ. Fish. Res. Bd. Canada, 32(3): 347-366.

____________ 1980 Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschi* and *T. inermis* (Crustacea. Euphausiacea). Journ. Plankton Res. 2(2): 129-143.

Samyshev, E.V. 1973 Relationships between trophic copepod groups in the zooplankton of the Gulf of Guinea. Hydrobiol. Journ. (Amer. Fish. Soc.), 9(4):25-32.

Scheuer, P.J. 1977 Chemical communication in Marine Invertebrates. Bioscience, 27(10):664-668.

Schmitt, W.L. 1939 Fresh-water jelly-fish records since 1932. Amer. Nat. 73(714):83-89.

Seapy, R.R. 1980 Predation by the epipelagic Heteropod Mollusk *Carinaria cristata* forma *japonica*. Mar. Biol., 60:137-146.

Sekiguchi, H. and T. Kato 1976 Influence of *Noctiluca's* predation on *Acartia* population in Ise Bay, Central Japan. Journ. Oceanogr. Soc. Japan, 32:195-198.

Sheader, M. and F. Evans 1975 Feeding and gut structure of *Parathemisto gaudichaudi* (Guerin) Amphipoda, Hyperiidea. Journ. Mar. Biol. Assoc. U.K. 55(3):641-656.

Shojima, Y. 1963 *Scyllarid* phyllosomas' habit of accompanying the jellyfish (Preliminary Report). Bull. Japanese Soc. Fish., 29(4):349-351.

Siegfired, C.A. and M.E. Kopache 1980 Feeding of *Neomysis mercedis* (Holmes). Biol. Bull. Mar. Biol. Lab. Woods Hole, 159:193-205.

Slabber, M. 1778 Naturkundige Verlustigingen Behelzende microscopise Waarneemingen van Inen mit-landse Water-en-Land Dieren Haarlem. Trans. by P.L. Mueller, pp.1-166.

Smedstad, O.M. 1972 On the biology of *Aglantha digitale rosea* (Forbes) (Coelenterata:Trachymedusae) in the Inner Oslofjord. Norwegian Journ. Zoology, 20 (2):111-135.

Smith, H.G. 1936 Contribution to the anatomy and physiology of *Cassiopea frondosa*. Paper Tortugas Lab., 31: 17-32.

Smith, R.E. and R.J. Kernehan 1981 Predation by the free-living Copepod *Cyclops bicuspidatus* Thomasi on larvae of striped bass and white perch. Estuaries, 21 (4):32-38.

Southward, A.J. 1955 Observations on the ciliary currents of the jelly-fish *Aurelia aurita*. Journ. Mar. Biol. Assoc. U.K. 34:201-216.

______________ 1962 The distribution of some plankton animals in the English Channel and approaches. II Surveys with the Gulf III High Speed Sampler, 1958-60. Journ. Mar. Biol. Assoc. U.K. 42:275-375.

Spallanzani, A.L. 1973 Viaggi alle due Scilie. 6 Vols.:1-272.

Spencer, A.N. 1975 Behabior and electrical activity in the hydrozoan *Proboscidactyla flavicirrata* (Brandt) II The Medusae. Biol. Bull., 1(149):236-250.

Steuer, A. 1910 Planktonkunde. Leipzig and Berlin. pp.1-723.

Stevenson, J.C. 1962 Distribution and survival of herring larvae (*Clupea pallasii* Valenciennes) in British Columbia waters. Journ. Fish. Res. Bd. Canada. 19:735-810.

Stone, J.H. 1969 The Chaetognatha community of the Agulhas Current; Its structure and related propieties. Ecol. Monogr. 39(4):433-463.

Strasburg, D.W. 1960 Estimates of larval tuna abundance in the Central Pacific. Fish. Bull. Fish. Wildl. Serv. 60:231-249.

Suárez-Caabro, J.A. 1955 Quetognatos de los mares Cubanos. Mem. Soc. Cubana Hist. Nat., 22(2):125-280.

Sullivan B.K. 1980 In situ feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station "P". Limn. Ocean., 25 (2):317-326.

Swanberg, N. 1974 The feeding behavior of *Beroë ovata*. Mar. Biol., 24:69-76.

Sveshnikov, V.A. 1963 The feeding habits of jelly fish as possible rivals of White Sea herring. Tr. Belomorsk. Biol. Stn. Mosk. Gos. Univ. 2:246-249.

Szyper, J.P. 1978 Feeding rate of the Chaetognatha *Sagitta enflata* in nature. Estuarine and coastal Marine Science, 7:567-575.

Takano, H. 1971 Breeding experiments of a marine littoral copepod *Tigriopus japonicus* Mori. Bull. Tokai Reg. Fish. Res. Lab., 64:71-80.

Tchindonova, J.G. 1959 Feeding of some groups of macrozooplankton in the North-western Pacific. Trudy Inst.

Okeanolog. ANSSSR, 30:166-189.

Terazaki, M. and R. Marumo 1982 Feeding habits of meso- and bathypelagic chetognatha, *Sagitta zetesios* Fowler. Oceanologica Acta 5(4):461-464.

Terazaki, M., M. Marumo and Y. Fujita 1977 Pigments of Meso- and bathypelagic Chaetognaths. Mar. Biol., 41: 119-125.

Tesch, J.J. 1949 Heteropoda. Dana Report (34):1-53.

Thayer, G.W., D.E. Hoss, M.A. Kjelson, W.F. Hettler and M.W. Lacroix 1974 biomass of zooplankton in the Newport River Estuary and the influence of Postlarval fishes. Chesapeake Sci., 15(1):9-16.

Theilacker, G.H. and R. Lasker 1973 Laboratory studies of predation by Euphausiid shrimps on fish larvae. Proc. Int. Symp. Early Life Hist. Fish, pp. 287-299.

Thomas, L.R. 1963 Phyllosoma larvae associated with Medusae. Nature, London, 198(4876):208.

Thomson, J.M. 1947 The Chaetognatha of South-eastern Australia. Counc. Sci. and Industry Res. Dic. Fish. Rept. (14):1-43.

Tokioka, T. 1939 Chaetognaths collected chiefly from the Bays of Sagami and Suruga with some notes on the shape and structure of the seminal vesicle. Rec. Ocean. Works Japan,10(2):123-150.

Totton, A.K. 1954 Siphonophora of the Indian Ocean, together with Systematic and biological notes on related specimens from other oceans. Discovery Rept., 27:1-162.

__________ 1960 Studies on *Physalia physalis* (L.). PART I, Natural History and morphology. Discovery Rept. 30:301-368.

Tsuruta, A. 1963 Distribution of plankton and its characteristics in the oceanic fishing ground, with special reference to their relation to fishery. Journ.

Shimonoseki College of Fish. 12(1):13-214.

Uchida, T. 1929 Studies on the Stauromedusae and Cubomedusae with special reference to their metamorphosis. Japan. Journ. Zool. 2:103-193.

Uschakov, P.V. 1972 Polychaetes. Polychaetes of the suborder Phyllodociformia of the Polar Basin and the north-western part of the Pacific (Families Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae and Lacydoniidae). Leningrad: Academy of Sciences of the USSSR, Zool. Inst. (Fauna of the USSR, n.s. No. 102). Vol. 1:1-259 (Transl. Israel Progrm Sci. Trans. Jerusalem, 1974).

Venter, G.E. 1969 The pilchard of Southwest Africa (*Sardinops ocellata*). The distribution of some chaetognaths and their relation to hydrographical conditions with special reference to the SW Africa region of the Benguela Current. Southwest Africa Mar. Res. Lab. Invest. Rept., (16):1-73.

Weldon, W.R.F. and G.H. Fowler 1890 Notes on recent experiments relating to the growth and rearing of food fish at the laboratory. I The rearing of lobster larvae. Journ. Mar. Biol. Assoc. U.K. 1(4):367-375.

Westernhagen H. von, and H. Rosenthal 1976 Predator-prey relationship between Pacific herring *Clupea harengus pallasi* larvae and a predator Hyperiid Amphipod, *Hyperoche medusarum*. U.S. Fish Bull. 74(3): 669-674.

Wickstead, J.H. 1959 A predatory copepod. Journ. Animal Ecology 28(1):69-82.

__________ 1962 Food and feeding in pelagic copepods. Proc. Zool. Soc. 139(4):545-555.

__________ 1965 An introduction to the study of tropical plankton. Hutchinson and Co. London, pp. 1-160.

Williams, M.H. 1961 An ecological survey of a scottish Herring Fishery. IV Changes in the plankton during the period 1949-1959. Bull. Mar. Ecolog., 5(48): 207-229.

Wilson, D.P. 1947 The Portuguese Man-of-war *Physalia physalis* L., in British and adjacent seas. Journ. Mar. Biol. Assoc. U.K., 27:139-172.

Wimpenny, K.S. 1937 The distribution, breeding and feeding of some important plankton organisms of the South west North Sea in 1934. I. *Calanus finmarchicus* (Gunn), *Sagitta setosa* (J. Müller) and *Sagitta elegans* (Verrill). Fish. Invest., London, Ser. 2, 15:1-52.

Yasuda, T. 1970 Ecological studies on the jelly-fish *Aurelia aurita* (L), in Urazoko Bay Fukin Prefecture. V. Vertical distribution of the Medusae. Ann. Rep. Noto Mar. Lab., 10:15-22.

Yen, J. 1982 Sources of variability in predation rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. Journ. Exp. Mar. Biol. Ecolog. 63: 105-117.

Zaitsev, Yu.P. 1968 La neustonologie marine; object, methods, realisations principales et problèmes. Pelagos, 8:1-48.

Zhuravlev, V.M. and M. Yu. Neyman 1976 Diurnal rhythm of the vertical migrations and feeding of *Parathemisto japonica* Bov. (Crustacea, Hyperiidae) in the Sea of Okhotsk. Oceanology, 16(2):193-195.

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LAS SURGENCIAS EN LA REGION DE CALIFORNIA-BAJA CALIFORNIA RELACIONES CON EL ZOOPLANCTON Y POBLACIONES DE *ENGRAULIS MORDAX* (PISCES)

Angeles Alvariño *

RESUMEN

Las zonas de surgencia se identifican por la presencia del Quetognato mesopelágico *Sagitta decipiens*, en los estratos batimétricos de los 0 m a los 100 m.

Sagitta decipiens abunda principalmente de la zona de los 225 m a los 475 m - 600 m de profundidad.

Las colecciones de plancton estudiadas corresponden a los cruceros mensuales realizados en aguas de California y Baja California en 1954, 1956, 1958. Estos años se caracterizan por temperaturas extremas, resultando así respectivamente, frío, extremadamente frío y cálido, con respecto a las condiciones climáticas normales en la región. También se han analizado las colecciones de plancton obtenidas con redes de apertura y cierre automáticos, durante las 4 estaciones del año 1969. Así se ocuparon día y noche en cada localidad ocho niveles batimétricos, desde 600 m hasta la superficie. De esta forma se pueden observar los cambios que ocurren en cada lugar en un mínimo de 12 horas de diferencia entre día y noche.

Se ha observado, que las zonas de surgencia se caracterizan por una notable diversidad de especies de Quetognatos, Sifonóforos y Medusas, y se discuten estas asociaciones planctónicas para 1954, 1956, 1958 y 1969.

Hay que señalar, que las larvas de *Engraulis mordax* (el pez más abundante en esta región) son escasas o están ausentes en las zonas de surgencia. Larvas de anchoa abundan en aguas caracterizadas por elevada densidad de poblaciones de *Sagitta euneritica*, *S. bierii*, *Muggiaea atlantica* y Copépodos.

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Varios mapas muestran la distribución de surgencias y larvas de anchoa, día y noche para cada estación del año 1969.

Las surgencias se presentaron con mayor intensidad en 1956 (en 35 lugares de los 316 ocupados, es decir, 11.1%), con mínimos en 1954 (en 12 de las 849 localidades ocupadas, 1.4%) y con intensidad intermedia en 1958 (en 46 de los 899 lugares ocupados, 5.1%).

Considerando tres categorías de abundancia de larvas (más de 241 larvas, menos de 241 y cero) se observó que durante los tres años (1954, 1956, 1958) *S. decipiens* aparecía en 2.8% de las capturas conteniendo más de 241 larvas, en 4.35% de las -- capturas con menos de 241 larvas y en 4.95% de las pescas carentes de larvas de anchoa.

En 1969 el número de arrastres en los estratos de los 0 m a los 100 m de profundidad han sido 256, y *S. decipiens* se presentó en 38, es decir, el 14.8%. Al parecer las surgencias han sido más activas en 1969 que en los otros años estudiados. La abundancia de *S. decipiens* en los estratos de 0m a 100 m de profundidad puede considerarse un índice del afloramiento y su intensidad, y así resulta, el invierno con mayor abundancia y frecuencia de este indicador planctónico, seguido del otoño, verano y primavera.

Las larvas de anchoa aparecían más frecuentes en primavera, y con mínimos en frecuencia y abundancia en el invierno.

Por lo tanto, la información obtenida indica una íntima relación inversa entre las surgencia y la abundancia de larvas de *E. mordax*, en la región de California-Baja California.

ABSTRACT

Upwelling locations are identified by the presence of the mesopelagic Chaetognatha *Sagitta decipiens* in the upper 0-100 m layers.

Sagitta decipiens is mainly abundant at the 225 to 475 or 600 m depth strata of the temperate and warm oceanic regions.

Plankton collections analyzed corresponded to monthly cruises of 1954, 1956, 1958 off California and Baja California.

These years were slightly colder, colder, and warmer than the long-term average for the California Current region. Plankton collections obtained with open-closing bongo nets were also analyzed, for the seasonal cruises of 1969. Hauls were obtained day and night at each location and eight depth strata, from 600 m to 0 m. Samples at each location and depth interval were only 12 hours apart.

It was found that upwelling coincided with a wide diversity of species of Chaetognatha, Siphonophorae and Medusae, and the pertinent planktonic associations are discussed for 1954, 1956, 1958, 1969.

Engraulis mordax larvae (the most abundant fish off California and Baja California) were in low concentration or obsent at upwelling locations. Anchovy larvae were abundant together with high density of *Sagitta euneritica*, *S. bierii*, *Muggiaea atlantica* and Copepods. This habitat is called "anchovy water".

Maps show the day/night seasonal distribution of upwelling and anchovy larvae, and profiles indicated the bathymetric distribution of *S. decipiens* and *E. mordax* during the 1969 seasonal periods.

Upwelling was more intense in 1956 (35 locations of 316 covered, that is 11.1%), minima in 1954 (12 of 849 locations occupied, 1.4%), and intermedian in 1958 (in 46 of 899 locations, 5.1%).

Anchovy abundance was divided into three categories: high (241 or more larvae per haul), low (1 to 240 larvae per haul), and zero, for the years 1954, 1956, 1958. *S. decipiens* appeared in 2.8 of collections with more than 240 larvae, in 4.35% of those with less than 241 larvae, and in 4.95% of hauls with no anchovy larvae.

During 1969, the number of hauls in the upper 100 m was 256, and *S. decipiens* was present in 38 of those, that is 14.8%. Apparently upwelling was more active in 1969 than in any of the other three years, 1954, 1956, 1958. The abundance of *S. decipiens* in the upper 100 m strata can be considered an indication of upwalling and of its intensity.

During 1969 upwelling was more frequent and intensive in winter, with minima in spring, and of intermedian magnitude in

fall and summer. Anchovy larvae appeared more frequent in spring, with minima in frequency and abundance in winter.

The information obtained show a close inverse relation between upwelling and abundance of *E. mordax* larvae in the California and Baja California regions.

INTRODUCCION

Sagitta decipiens es un quetognato mesopelágico que ocupa estratos de la zona batimétrica de los 200 a los 1000 m, en las regiones templadas y cálidas oceánicas (Alvariño, 1965a). La presencia de esta especie en la zona epipelágica, puede considerarse indicación de fenómenos de surgencia (Alvariño, 1965b; Nair, 1977; Nair y Rao, 1973, y otros autores).

Se ha analizado la distribución de *S. decipiens* en las zonas del epiplancton, en las colecciones mensuales obtenidas desde 140 m de profundidad hasta la superficie, frente a California y Baja California, durante los años 1954, 1956, 1958; y la distribución batimétrica de esta especie se ha determinado mediante el estudio de las colecciones de plancton efectuadas a ocho niveles de profundidad (desde 600 m hasta 0 m) en la misma región y durante las 4 estaciones del año 1969.

Se trata de obtener con estos estudios, una información más amplia y detallada en relación con los fenómenos de surgencia, las asociaciones planctónicas correspondientes, y la supervivencia de larvas de *E. mordax*. Alvariño (1979) ha observado que las larvas de anchoa aparecían en escasa concentración o estaban ausentes en las zonas de surgencia.

METODOS

Las colecciones mensuales de los años 1954, 1956, 1958 se obtuvieron con redes cónicas de 1 metro de diámetro en la boca y unos 5 m de longitud, con malla de 500 µ. Los arrastres fueron oblicuos, desde unos 140 m de profundidad, o menos en zonas someras, hasta la superficie.

Las colecciones de 1969 se obtuvieron con redes pares bongo, de apertura y cierre automáticos, y malla de 505µ y 303µ.

Las capturas en 1969 se realizaron a mediodía y media noche, en cada localidad y estrato batimétrico. De esta forma se obtienen datos en los dos períodos del día, con una diferencia mínima de 12 horas. Estas colectas abarcaron las cuatro estaciones del año, con cruceros en invierno (Febrero-Marzo, 6902-03), primavera (Mayo-Junio, 6905-06), verano (Agosto-Septiembre, 6908-09), otoño (Noviembre-Diciembre, 6911-12).

Se analizó en cada caso la totalidad de la muestra de plancton, determinándose el número de individuos para cada especie de Quetognatos, Sifonóforos, Medusas, Ctenóforos, Condróforos, larvas de peces, y también se anotaron otras poblaciones que aparecían en notable abundancia en el plancton. Los valores numéricos para cada especie se calcularon para 1000 m^3 de agua, con objeto de poder comparar dichos datos. Los arrastres oblicuos ocuparon los ocho estratos batimétricos desde 600-475m, 475-350 m, 350-225 m, 225-100 m, 100-75 m, 75-50 m, 50-25 m, 25-0 metros.

En este trabajo se incluyen en la discusión especies de Quetognatos, Sifonóforos, Medusas y larvas de *Engraulis mordax* (el pez más abundante en California y Baja California).

La presencia de *S. decipiens* en las colecciones efectuadas en 1954, 1956, 1958, que comprendían de los 140 m hasta la superficie, sirve adecuadamente para señalar fenómenos de surgencia. En 1969, cuando *S. decipiens* aparece en las muestras procedentes de arrastres efectuados de los 100 a los 0 m, se considera indicadora de surgencia. Sin embargo, no se puede identificar adecuadamente la surgencia por la presencia de *S. decipiens* de los 225 m a los 100 m de profundidad, ya que la operación abarca también estratos de la zona mesopelágica.

SURGENCIAS Y ABUNDANCIA DE LARVAS DE *ENGRAULIS MORDAX*

La presencia de *Sagitta decipiens* (Quetognato mesopelágico) en las colecciones mensuales de 1954, 1956, 1958, obtenidas desde 140 m hasta la superficie oceánica, se considera indicadora de surgencia de aguas profundas. Las colecciones de plancton correspondientes a 1969 sirven para señalar la distribución batimétrica de esta especie y la estructura de las zonas de surgencia en las regiones de California y Baja California.

Los años 1954, 1956, 1958 se caracterizaron por temperaturas extremas, resultando así respectivamente más frío, extremadamente frío y cálido, con respecto a las condiciones climáticas normales de la región.

En los estudios sobre la abundancia de depredadores planctónicos en relación con la concentración de larvas de *E. mordax* (el pez más abundante en estas regiones) se observó que en general la presencia de *S. decipiens* en los estratos del epiplancton coincidía con escasez o ausencia de larvas de anchoa (Alvariño, 1979).

Se consideraron tres categorías de abundancia de larvas de anchoa, más de 240 larvas por colecta, menos de 241 y cero. Durante los años 1954, 1956, 1958, se analizaron un total de 2064 muestras, y *S. decipiens* aparecía en 93. En 1954 se analizaron 849 muestras y *S. decipiens* se presentó en 12, o sea el 1.4%; en 1956 se estudiaron 316 muestras y *S. decipiens* aparecía en 35, o sea 11.1%, y de las 899 colecciones correspondientes a 1958, *S. decipiens* se encontró en 46, o sea el 5.1%.

Tomando *S. decipiens* como base para determinar las surgencias, este fenómeno resultaba más intenso o frecuente en 1956 que en los otros dos años, en cuantía mínima en 1954, e intermedia en 1958 (Alvariño, 1979), lo cual concuerda con los resultados obtenidos por Bakun (1973) y Wyllie (1966) utilizando métodos físico-matemáticos.

La frecuencia, o sea el número de ocasiones en que aparece la especie con respecto a la cuantía de operaciones efectuadas, es un dato probablemente más adecuado que la cantidad total de ejemplares colectados, ya que a veces aparecen extremadamente abundantes en una localidad, y esa cantidad afecta al promedio total, aún cuando la abundancia en una localidad señale que se estaba produciendo ahí una surgencia intensa.

No obstante, basándose en la abundancia de *S. decipiens* se determinó un promedio de 10 para 1956, 4.1 para 1954, y 1.9 en 1958 (Alvariño, 1979). En el otoño de 1956 las surgencias se presentaban más acusadas, en 1958 las estaciones con máximos resultaron en primavera, y en el invierno de 1954. De los 256 arrastres efectuados día y noche en la zona de los 100 a 0 m durante 1969, *S. decipiens* aparecía en 38, es decir en un 14.8%. Al parecer durante 1969 los fenómenos de surgencia fueron más activos que en los otros tres años.

Al comparar la distribución de *S. decipiens* y larvas de anchoa durante los años 1954, 1956, 1958, se observó que *S. decipiens* coincidía con elevada concentración de larvas (más de 240) en 2.8% de casos, con escasa cantidad de larvas (menos de 241) en 4.35%, y con ausencia de larvas en 4.95% de casos; lo cual podría interpretarse que abundancia de larvas de anchoa no es frecuente en zonas de surgencia (Alvariño, 1979).

El análisis de las colecciones batimétricas de 1969 documenta sobre la distribución de *S. decipiens* desde la superficie oceánica hasta los 600 m de profundidad en las regiones de California y Baja California. Este estudio detalla la distribución batial de la especie en el ámbito oceánico en relación con los períodos diurno y nocturno, y en las cuatro estaciones del año. Durante 1969 se observaron 31 localidades (día y noche) en donde la surgencia aparecía señalada por la presencia de *S. decipiens*, y solamente en 9 de esas localidades se encontraron larvas de *E. mordax*, 29%, en escasa concentración. (Tablas 1 y 2).

En las localidades con surgencia en donde concurrían larvas de anchoa, éstas aparecían en escasa cantidad y solamente en los estratos cercanos a la superficie oceánica, y al mismo tiempo la surgencia estaba señalada por un escaso número de *S. decipiens*, lo que podría considerarse como indicio de afloramiento débil.

En la mayor parte de las localidades con fuerte surgencia, identificadas por la abundancia de *S. decipiens* no se encontraron larvas de anchoa.

En una localidad con elevada concentración de larvas de anchoa, Estación 90.45 del crucero de verano, se observaron más de 3,000 larvas en una colecta nocturna a los 25-0 m de profundidad. En esta localidad no se observó surgencia.

Larvas de *E. mordax* aparecían en 7 de las 23 localidades (día y noche) identificadas por una surgencia débil (30.43%) y en 2 de otras 15 localidades con fuerte surgencia (13.3%), - mientras que estas larvas estaban ausentes en 29 localidades con surgencia (39.1%), durante 1969.

Hay que hacer notar además, que la indicación de surgencias alcanza en la mayor parte de los casos hasta los 100-75 m de profundidad, seguido por los 75-50 m y 50-25 m, y que sin embargo las larvas de anchoa aparecían preferentemente a los 25-0 m de profundidad y con escasa frecuencia en otros estratos de la zona entre los 100 y 0 m de profundidad. (Figs. 1,2,3,4).

En 1969 las surgencias más frecuentes e intensas (en relación con la presencia de *S. decipiens* en los 100-0 m) en el invierno (Tabla 3) y con mínimos en frecuencia e intensidad en primavera, mientras que el valor de la frecuencia era mayor en el otoño que en el verano, y el promedio de abundancia era más elevado en el verano que en el otoño.

La distribución de las larvas de *E. mordax* indicaba una mayor frecuencia en la primavera con mínimos en frecuencia y promedio de abundancia en el invierno (Tabla 4). Estos valores se relacionan inversamente con la distribución de las surgencias. Sin embargo los valores de abundancia de larvas no se corresponden con las frecuencias en primavera, verano y otoño. Como ya se ha indicado, la frecuencia resulta ser un valor más realístico, pues el promedio de abundancia puede alterarse notablemente con una captura abundante en una sola localidad, como sucedió en el verano de 1969 (Estación 90.45 contenía más de 3,000 larvas).

DISTRIBUCION DE *E. MORDAX* Y DE *S. DECIPIENS* EN RELACION CON LAS NOTACIONES HIDROGRAFICAS

Se analizaron los datos hidrográficos, temperatura, salinidad y oxígeno correspondientes a las localidades con larvas de anchoa, y aquellas en donde aparecía *S. decipiens* en los estratos de los 100 m a los 0 m de profundidad, durante 1969. En el caso de *S. decipiens* se seleccionaron exclusivamente las localidades donde no aparecían larvas de anchoa.

Las notaciones correspondientes de temperatura, salinidad y oxígeno en los estratos ocupados por larvas de anchoa aparecen en la Tabla 5.

Al analizar la distribución batimétrica de las larvas de anchoa y los perfiles hidrográficos correspondientes, se ha podido observar que las larvas aparecían con mayor frecuencia precisamente en la zona de la termoclina, y en el resto de los casos indistintamente por encima o por debajo de esta estructura térmica.

La mayor concentración de larvas de anchoa obtenida en un arrastre nocturno en verano (Estación 90.45) a los 25-0 m de - profundidad (Tabla 2) se caracterizaba por una temperatura de 16°C a 18.64°C, salinidad de 33.6 a 33.8 o/oo y oxígeno de 4.7

a 5.8 ml por litro. Esta concentración de anchoas aparecía por encima de la termoclina.

Al parecer el habitat más adecuado para las larvas de anchoa en las regiones de California y Baja California se caracteriza por una temperatura relativamente elevada, salinidades bajas y elevada concentración de oxígeno.

Las notaciones de temperatura, salinidad y oxígeno en los estratos de menos de 100 m de profundidad habitados por *S. decipiens*, pero con ausencia de larvas de anchoa, se detallan en la Tabla 6, conjuntamente con las respectivas notaciones para los estratos con mayor concentración de esta especie. Como puede observarse, las notaciones son sensiblemente bastante similares en la mayor parte de los casos.

Las poblaciones de *S. decipiens* se extendían siempre por debajo de la termoclina.

EL PLANCTON EN LAS ZONAS DE SURGENCIA Y EN EL HABITAT DE *E. MORDAX*

Se identificaron las localidades con elevada concentración de anchoa durante 1969 y se determinaron las especies de Quetognatos, Sifonóforos y Medusas que ahí concurrían. Así, en la estación 90.45, del crucero de verano (6908-09) aparecían, según ya se indicó, más de 3,000 larvas de anchoa en los estratos de 25-0 m de profundidad. En esta misma localidad se observaron 38,320 individuos de *S. euneritica* (la mayoría juveniles), varios centenares de *Muggiaea atlantica* y decenas de *S. enflata* y *S. minima*, junto con una enorme cantidad de copépodos calanoides. Esta es la fauna característica de las aguas de anchoa (Alvariño, 1979).

Seleccionando las localidades con elevada concentración de *S. decipiens* en los años 1954, 1956, 1958, se han determinado las especies de Quetognatos, Sifonóforos y Medusas que integraban las correspondientes colecciones. Se relacionaron dichas asociaciones de especies con la presencia o ausencia de larvas de anchoa durante dichos años y los resultados aparecen en la (Tabla 7). Asimismo se analizaron para 1969 las asociaciones de Quetognatos, Sifonóforos y Medusas en las zonas de fuerte surgencia, determinada por una elevada cantidad de *S. decipiens* en los estratos de 100 a 0 m de profundidad. Estas localidades se caracterizan por una concentración de elevada diversidad de especies (*S. scrippsae*, *S. bipunctata*, *S. enflata*, *S. hexaptera*, *S. maxima*, *S. minima*, *S. pacifica*, *S. pseudoserratodentata*, *S. zetesios*, *Pterosagitta draco*, *Krohnitta subtilis*, *Eukrohnia hamata*, *Lensia challengeri*, *L. conoidea*, *L. cossack*, *L. exeter*, *L. hotspur*, *L. multicristata*, *Diphyes bojani*, *Diphyopsis mitra*, *Hippopodius hippopus*, *Physophora hydrostatica*, *Athorybia rosacea*, *Nectodroma reticulata*, *Phialopsis diegensis*, *Aeginura grimaldii*, *Aglantha digitale*, *Leuckartiara zacae*, *Liriope tetraphylla*, *Rhopalonema velatum*, *Atolla wyvillei*, *Atorella vanhoeffeni*.

Esta elevada concentración de especies no es ocasionada únicamente por el afloramiento de aguas profundas, sino que además ha de ser producida por convergencia de remolinos de diversas amplitudes.

Sagitta decipiens aparecía con máximas concentraciones, más de 10,000 individuos en estratos de 125 m de amplitud, o sea, más de 2,000 ejemplares en cada estrato de 25 m en esa zona, a los 225-350 m de profundidad en primavera, verano y otoño, y también a 350-475 m en primavera y otoño, y a 600-475 m de profundidad en el otoño. Las especies de Quetognatos, Sifonóforos y Medusas concurrentes en estas zonas de elevada concentración de *S. decipiens*, aparecen en la Tabla 8.

Resumiendo, los resultados obtenidos indican que la mayor frecuencia e intensidad de surgencias ocurría en el invierno de 1969 y en esta época se observaron mínimos de anchoa tanto en frecuencia como en promedio de individuos. La máxima frecuencia de anchoas ocurría en primavera, coincidiendo con mínimas surgencias. No obstante el promedio máximo de la población de anchoas se presentaba en verano (resultado de una gran concentración de larvas en una sola localidad). Por lo tanto, en general se puede indicar que la concentración de larvas de anchoa aparece en razón inversa en relación con las zonas de surgencia, en las regiones de California y Baja California.

También se confirma que la supervivencia de las larvas de anchoa llega al máximo en el habitat característico de la especie, con escasez de depredadores y abundante alimento (Copépodos pequeños), integrado además por las especies *S. euneritica y M. atlantica*.

Además se señala que las zonas de surgencia están caracterizadas por una confluencia elevada de diversas especies, no solamente procedentes de los estratos profundos, sino también de las zonas adyacentes a la localidad de surgencia, arrastradas por remolinos de variada amplitud que convergen o entrecruzan en las localidades de la surgencia.

TABLA 1. DISTRIBUCION DE S. *decipiens* EN CALIFORNIA Y BAJA CALIFORNIA, 1969.

Est. / Prof. m	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Total promedio		Total promedio (100 m)	
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
6902-03																										
25- 0	0	0	0	0	-	-	-	-	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0
50- 25	-	0	0	0	-	-	-	-	20	0	0	0	-	-	0	0	-	0	0	0	0	0	3	0	3	0
75- 50	0	-	312	-	-	-	-	-	346	28	0	1692	-	-	0	0	-	0	0	0	-	-	109	344	109	349
100- 75	0	-	10	-	-	-	-	-	1806	7588	270	755	-	-	195	0	14	0	134	5	16	0	305	1391	305	1391
225-100	-	-	1660	-	-	-	-	-	4684	-	3194	-	-	-	6452	-	-	452	-	4525	649	6	3327	1661		
350-225	-	-	4345	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6462	-	5403	-		
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
6905-06																										
25- 0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50- 25	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0
75- 50	0	0	0	0	0	0	-	0	-	0	0	0	0	0	18	0	0	0	16	0	0	0	3	0	3	0
100- 75	0	7	0	0	0	0	-	20	-	0	0	0	-	0	202	26	-	0	-	0	-	0	40	4	40	4
225-100	420	4860	2100	350	0	5810	0	265	-	0	80	0	-	0	140	475	330	120	620	1240	-	20	461	1314		
350-225	-	6270	8920	6670	4205	7140	3025	3305	-	9320	735	3390	-	-	10	550	2710	665	17040	-	-	295	5235	4178		
475-350	635	285	1810	285	1360	495	3740	455	-	190	785	70	-	38060	1695	105	105	85	445	90	275	0	1205	3647		
600-475	50	5	20	150	25	10	-	110	-	45	150	160	-	0	690	325	5	-	1155	1965	-	0	299	278		
6908-09																										
25- 0	-	-	-	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50- 25	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0
75- 50	-	-	-	4	0	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0
100- 75	-	-	-	28	690	49	0	-	0	0	6	0	0	0	0	1	125	150	0	2	0	0	91	25	91	25
225-100	1215	-	470	115	5785	-	555	1065	-	705	1455	940	75	0	3560	3240	2745	680	75	655	1140	60	1707	829		
350-225	1510	-	1425	4220	4980	4120	10	6555	-	-	9650	3150	-	-	-	13020	480	-	3310	540	1255	1245	2827	4692		
475-350	180	-	40	85	135	1495	4285	1845	2035	1945	2620	23905	1005	1885	2885	6300	2350	1210	305	2665	2555	1635	1672	4297		
600-475	0	-	-	-	-	-	-	-	370	30	100	1020	150	85	2260	0	40	5	20	0	45	15	373	165		
6911-12																										
25- 0	0	0	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50- 25	0	0	0	-	-	-	-	-	0	-	0	0	0	-	0	0	-	0	0	0	0	0	0	0	0	0
75- 50	0	0	0	-	-	-	-	-	-	-	0	16	0	-	0	0	124	-	0	0	0	0	15	3	15	3
100- 75	0	-	293	-	-	-	-	-	1	32	2	-	-	-	-	15	-	0	2	0	0	0	49	9	49	9
225-100	-	6685	3425	-	-	-	-	-	-	-	7840	-	1230	420	1470	2130	-	130	1390	-	305	245	2610	1922		
350-225	835	1240	655	-	-	-	-	-	-	-	5110	29675	-	-	630	1990	1640	1610	4050	3925	-	4035	2163	7079		
475-350	840	690	980	-	-	-	-	-	-	-	4850	0	1665	-	580	95	130	100	865	-	245	510	1269	348		
600-475	770	11505	0	-	-	-	-	-	-	-	-	2600	-	-	9060	15	15	15	20	0	115	15	1663	2358		

D= Colecciones diurnas
N= Colecciones nocturnas

TABLA 2. DISTRIBUCION DE LARVAS DE *Engraulis mordax* EN CALIFORNIA Y BAJA CALIFORNIA, 1969.

Est. / Prof. m	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Promedio Total	
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	Dia	Noche
6902-03																								
25- 0	0	4	0	0	-	-	-	-	0	0	0	0	-	-	0	0	0	0	0	1	0	0	0	0.5
50- 25	-	4	0	0	-	-	-	-	0	0	0	0	-	-	0	0	-	0	0	0	0	0	0	0.5
75- 50	0	-	0	-	-	-	-	-	0	0	0	0	-	-	0	0	-	0	0	0	-	-	0	0
100- 75	0	-	0	-	-	-	-	-	0	15	0	0	-	-	0	0	0	0	0	0	0	0	0	2
225-100	-	-	0	-	-	-	-	-	0	-	0	-	-	-	0	-	-	0	-	0	0	0	0	0
350-225	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
6905-06																								
25- 0	1	0	0	0	0	0	0	0	-	1	0	1	0	0	0	21	0	36	0	4	0	0	0.1	6.3
50- 25	0	1	0	0	0	0	-	0	-	0	0	0	0	0	6	17	1	3	4	9	-	0	1.3	3
75- 50	0	0	0	0	0	0	-	0	-	0	2	0	0	0	0	30	16	1	1	0	0	0	2	3
100- 75	0	0	0	0	0	0	-	0	-	0	0	0	-	0	0	0	-	1	-	0	-	0	0	0
225-100	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0	0	0	0	0	-	0	0	0
350-225	-	0	0	0	0	0	0	0	-	0	0	0	-	-	0	0	0	0	0	-	-	0	0	0
475-350	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0
600-475	0	0	0	0	0	0	-	0	-	0	0	0	-	0	0	0	0	-	0	0	-	0	0	0
6908-09																								
25- 0	-	-	-	0	-	0	-	10	0	>3000	11	1	0	20	0	0	0	0	0	0	0	0	1.5	303
50- 25	-	-	-	0	0	0	0	0	0	0	0	5	0	0	0	0	-	0	0	0	0	0	0	0.5
75- 50	-	-	-	0	0	0	0	0	0	0	-	1	0	20	0	0	0	-	0	0	0	0	0	2.3
100- 75	-	-	-	0	0	0	10	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.1	0
225-100	0	-	0	0	0	-	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
350-225	0	-	0	0	0	0	0	0	-	-	0	0	-	-	-	0	0	-	0	0	0	0	0	0
475-350	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
600-475	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6911-12																								
25- 0	0	0	0	-	-	-	-	-	0	0	0	0	0	20	10	80	0	12	0	0	0	0	1.1	14
50- 25	0	0	0	-	-	-	-	-	0	-	0	0	0	-	18	200	-	100	0	0	0	0	2.2	50
75- 50	0	0	0	-	-	-	-	-	-	-	0	0	0	-	100	200	0	-	11	0	0	0	13.8	40
100- 75	0	-	0	-	-	-	-	-	0	0	0	-	-	-	-	200	-	20	0	0	0	0	0	44
225-100	-	0	0	-	-	-	-	-	-	-	0	-	0	0	0	0	-	0	0	-	0	0	0	0
350-225	0	0	0	-	-	-	-	-	-	-	0	0	-	-	0	0	0	0	0	0	-	0	0	0
475-350	0	0	0	-	-	-	-	-	-	-	0	0	0	-	0	0	0	0	0	-	0	0	0	0
600-475	0	0	0	-	-	-	-	-	-	-	-	0	-	-	0	0	0	0	0	0	0	0	0	0

D= Colecciones diurnas

N= Colecciones nocturnas

TABLA 3. DISTRIBUCION DE S. *decipiens* EN LOS ESTRATOS DE 0 A 100 m. DE PROFUNDIDAD.

Crucero	Número de arrastres	Arrastres conteniendo S. *decipiens*	%	Cantidad de S. *decipiens* en esas muestras	Promedio de S. *decipiens*
Invierno (6902-03)	55	15	27.2	13,171	239
Primavera (6905-06)	76	6	7.8	289	3.8
Verano (6908-09)	70	9	12.8	1055	15.7
Otoño (6911-12)	55	8	14.5	485	5.0

TABLA 4. DISTRIBUCION DE LARVAS DE E. *mordax* EN LAS CUATRO ESTACIONES DE 1969.

Crucero	Número de arrastres	Arrastres conteniendo larvas de E. *mordax*	%	Cantidad de E. *mordax* en estas muestras	Promedio de larvas de E. *mordax*
Invierno (6902-03)	55	4	7	24	0.43
Primavera (6905-06)	76	19	25	156	2
Verano (6908-09)	70	9	12.8	3,100	44
Otoño (6911-12)	55	11	20	1,671	30

TABLA 5. NOTACIONES HIDROGRAFICAS EN LOS ESTRATOS HABITADOS POR LARVAS DE E. *mordax*.

Crucero	Temperatura °C	Salinidad o/oo	Oxígeno ml por litro
Invierno (6902-03)	10.39 a 17.1	33.52-34.20	3.33-5.99
Primavera (6905-06)	10.3 a 17.7	32.70-33.70	3.20-6.5
Verano (6908-09)	12.46 a 18.8	33.1 -33.9	4.7 -6.1
Otoño (6911-12)	11.33 a 20.45	33.64-34.02	3.0 -5.63

TABLA 6. NOTACIONES HIDROGRAFICAS EN LOS ESTRATOS DE 100-0 m. HABITADOS POR *Sagitta decipiens*, ZONAS DE SURGENCIA, Y CON AUSENCIA DE LARVAS DE E. *mordax*.

Estación del año	Temperatura °C	Salinidad o/oo	Oxígeno ml por litro
Invierno (6902-03)	9.5 a 16.39	33.27-33.95	3.28-6.04
Primavera (6905-06)	11.8 a 12.03	33.00-33.2	5.09-6.2
Verano (6908-09)	8.8 a 15.59	32.9 -33.8	3.2 -6.03
Otoño (6911-12)	9.14 a15.46	32.11-33.6	4.31-5.58

Notaciones hidrográficas en los estratos con máxima concentración de *S. decipiens*

Estación y Profundidad	Temperatura °C	Salinidad o/oo	Oxígeno ml por litro
Primavera 225-350m	8 a 9.2	33.5 -34.0	0.70-2.0
Verano 225-475m	5.89 a 11.0	33.5 -34.2	0.77-2.0
Otoño 225-350	7.0 a 8.56	34.0 -34.1	1.0 -3.0

TABLA 7. DEPREDADORES PLANCTONICOS EN ZONAS DE SURGENCIA (CARACTERIZADAS POR S. *decipiens*), Y CON ESCASO NUMERO, O AUSENCIA DE LARVAS DE E. *mordax*.

Crucero Larvas de anchoa	Invierno 5401-5403	Primavera 5404-5406	Verano 5407-5409	Otoño 5410-5412
Ausentes	S. *Bierii* S. *Bipunctata* S. *enflata* S. *euneritica* S. *hexaptera* S. *pacifica* S. *scrippsae* Ch. *appendiculata* D. *dispar* L. *tetraphylla* R. *velatum*		S. *Bierii* S. *bipunctata* S. *hexaptera* S. *pacífica* S. *scrippsae* Ch. *appendiculata* D. *dispar* R. *velatum* *Beroe*	S. *Bierii* S. *bipunctata* S. *enflata* S. *eneritica* S. *hexaptera* S. *Pacífica* S. *scrippsae* M. *atlantica* Ch. *appendiculata* D. *dispar* L. *tetraphylla* R. *velatum* *Beroe*
Escaso número		S. *euneritica* M. *atlantica* R. *velatum*		
Cruceros:	Invierno 5601-5603	Primavera 5604-5606	Verano 5607-5609	Otoño 5610-5612
Ausentes		S. *bierii* S. *bipunctata* S. *enflata* S. *hexaptera* S. *pacífica* S. *scrippsae* Ch. *appendiculata* L. *tetraphylla* R. *velatum* *Beroe*	S. *bierii* S. *euneritica* S. *hexaptera* S. *pacífica* M. *atlantica* D. *dispar* *Beroe*	S. *bierii* S. *bipunctata* S. *enflata* S. *euneritica* S. *hexaptera* S. *scrippsae* Ch. *appendiculata* D. *dispar* L. *tetraphylla* R. *velatum* *Beroe*
Escaso número	S. *Bierii* S. *enflata* S. *euneritica* S. *hexaptera* S. *pacífica* M. *atlantica* R. *velatum*			
Cruceros:	Invierno 5801-	Primavera 5804-5806	Verano 5807-5809	Otoño 5810-5812
Ausentes	S. *enflata* S. *hexaptera* S. *pacífica* M. *atlantica* Ch. *appendiculata* D. *dispar* L. *tetraphylla* R. *velatum* A. *hemistoma* *Beroe*	S. *bierii* S. *bipunctata* S. *enflata* S. *pacífica* S. *scrippsae* M. *atlántica* Ch. *appendiculata* D. *dispar* L. *tetraphylla* A. *hemistoma* *Beroe*		S. *bierii* S. *bipunctata* S. *enflata* S. *hexaptera* S. *pacífica* S. *scrippsae* Ch. *appendiculata* L. *tetraphylla* R. *velatum* A. *hemistoma*
Escaso número			S. *euneritica* S. *scrippsae*	

TABLA 8. ESPECIES DE QUETOGNATOS, SIFONOFOROS Y MEDUSAS, CONCURRENTES CON MAXIMAS CONCENTRACIONES DE *Sagitta decipiens*.

Crucero, Estación, Localidad Etc.	Especies Asociadas con *Sagitta decipiens*		
	Quetognatos	Sifonóforos	Medusas
Crucero 6905-06 Estación 120.70 colecta diurna Profundidad: 225-350 m	*S. bierii* *S. enflata* *S. hexaptera* *S. minima* *S. pseudoserratodentata* *k. subtilis*	*Chelophyes appendiculata*	
Crucero 6908-09 Estación 90.60 colecta nocturna Profundidad: 350-475,	*S. scrippsae* *S. maxima* *S. minima* *S. zetesios* *K. subtilis* *E. hamata*	*L. conoidea* *L. multicristata* *L. ajax* *L. reticulata* *Chuniphyes multidentata* *Stephanomia bijuga*	*Rhopalonema velatum* *Aeginopsis laurentii*
Estación 120-45 Colecta nocturna Profundidad: 225-350 m	*S. scrippsae* *S. maxima* *S. bierii* *K. subtilis*	*L. challengeri* *Ch. multidentata*	*Colobonema sericeum*
Crucero 6911-12 Estación 90.60 colecta nocturna Profundidad: 225-350 m	*S. scrippsae* *S. maxima* *S. zetesios* *K. subtilis* *E. hamata*	*L. conoidea* *S. bijuga*	*Solmaris corona*

LEYENDAS DE LAS FIGURAS

Fig. 1. Relaciones entre la distribución batimétrica de larvas de *Engraulis mordax* y del Quetognato *Sagitta decipiens*, especie indicadora de surgencias. Febrero-Marzo de 1969. Las colecciones de plancton han sido obtenidas en las mismas localidades aproximadamente a las doce del día y de la noche.

Fig. 2. Relaciones entre la distribución batimétrica de larvas de *Engraulis mordax* y del Quetognato *Sagitta decipiens*, especie indicadora de surgencias. Mayo-Junio de 1969. Las colecciones de plancton han sido obtenidas en las mismas localidades aproximadamente a las doce del día y de la noche.

Fig. 3. Relaciones entre la distribución batimétrica de larvas de *Engraulis mordax* y del Quetognato *Sagitta decipiens*, especie indicadora de surgencias. Agosto-Septiembre de 1969. Las colecciones de plancton han sido obtenidas en las mismas localidades aproximadamente a las doce del día y de la noche.

Fig. 4. Relaciones entre la distribución batimétrica de larvas de *Engraulis mordax* y del Quetognato *Sagitta decipiens*, especie indicadora de surgencias. Noviembre-Diciembre de 1969. Las colecciones de plancton han sido obtenidas en las mismas localidades aproximadamente a las doce del día y de la noche.

BIBLIOGRAFIA

Alvariño, A. 1965a Chaetognaths. Mar. Biol. and Ocean., Annual Rev., 3:115-194.

____________ 1965b Distributional ATLAS of Chaetognatha in the California Current Region during CalCOFI monthly cruises of 1954 and 1958. Calif. Coop. Ocean. Fish. Invest. ATLAS 3:I-XIII+ 1-291.

____________ 1979. The relation between the distribution of Zooplankton predator and anchovy larvae. ICES, Early Life History of Fish, Symp. April, 1979, Woods Hole, Massachusetts.

Bakun, A. 1973. Coastal upwelling indices west coast of North America, 1946-1971. NOAA Techn. Rept. NMFS, SSRF-671:1-103.

Nair, V.R. 1977. Chaetognatha of the Indian Ocean. Proc. Symp. Warm Water Zooplankton, Suppl. UNESCO/ NIO, pp. 168-195.

____ and T.S.S. Rao 1973 Chaetognatha of the Arabian Sea. IN: Ecolog. Stud. Analysis and Synthesis, Ed. B. Zeitzschel, 3(4.6):293-544.

Wyllie, J.G. 1966. Geostrophic flow of the California Current at the surface and at 200 m. CalCOFI Atlas 4:I-XIII+1-288.

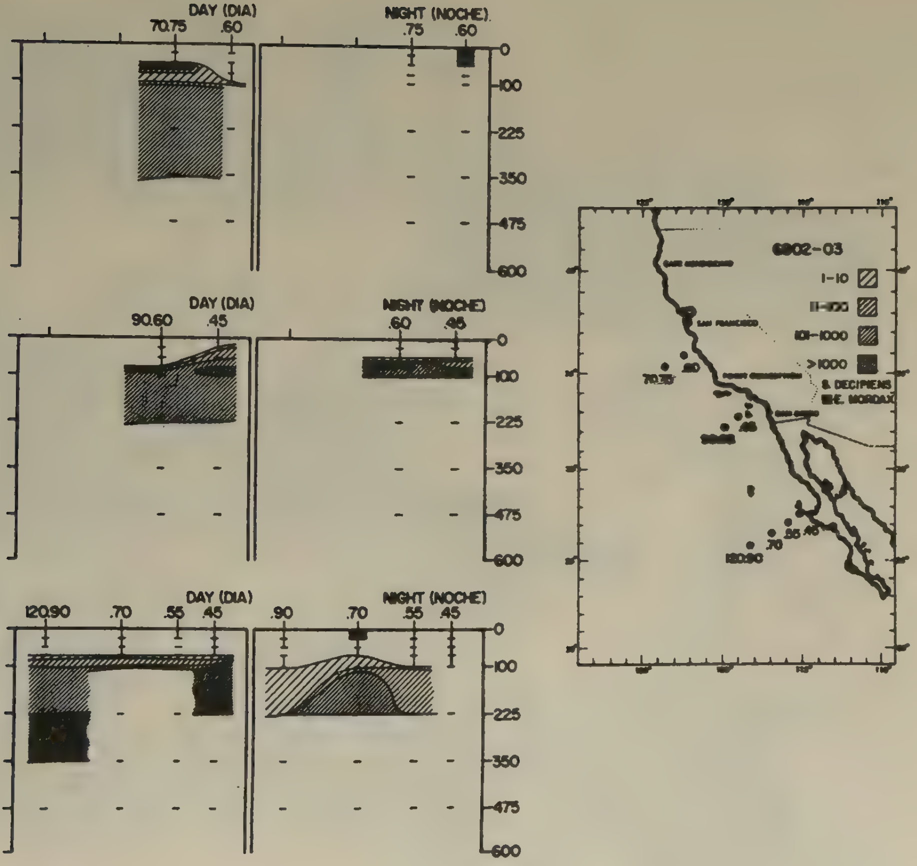

Fig. 1. Las surgencias en la region de California-Baja California. Relaciones con el zooplancton y poblaciones de *E. mordax*.

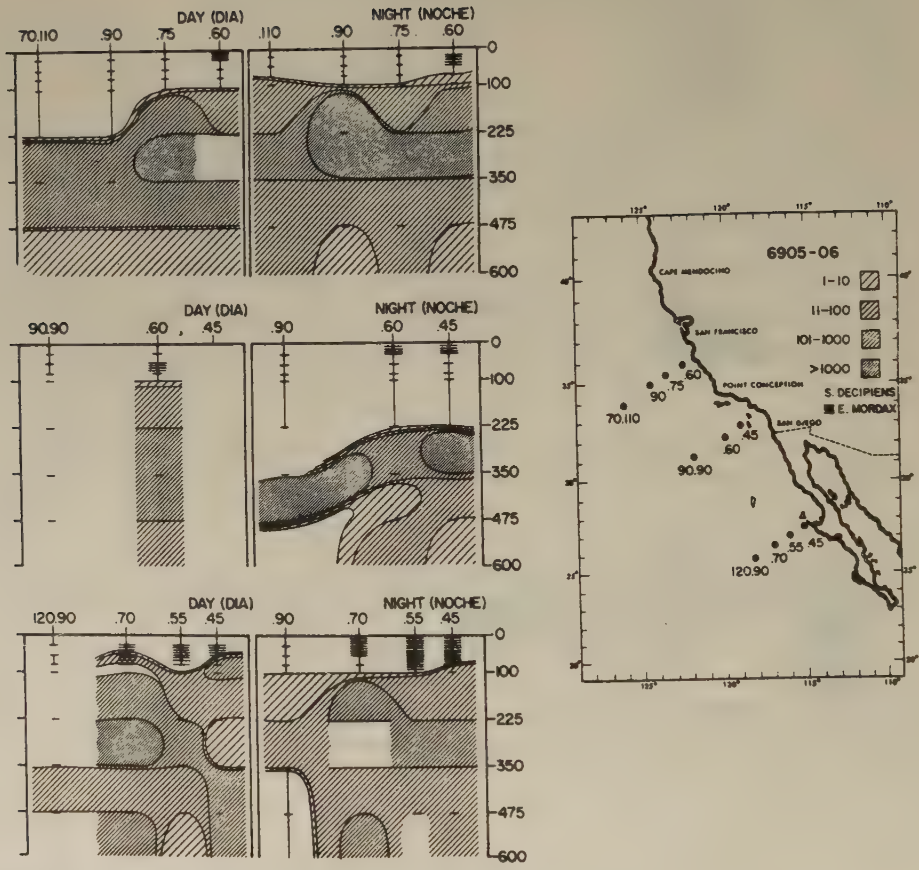

Fig. 2. Las surgencias en la región de California-Baja California. Relaciones con el zooplancton y poblaciones de *E. mordax*.

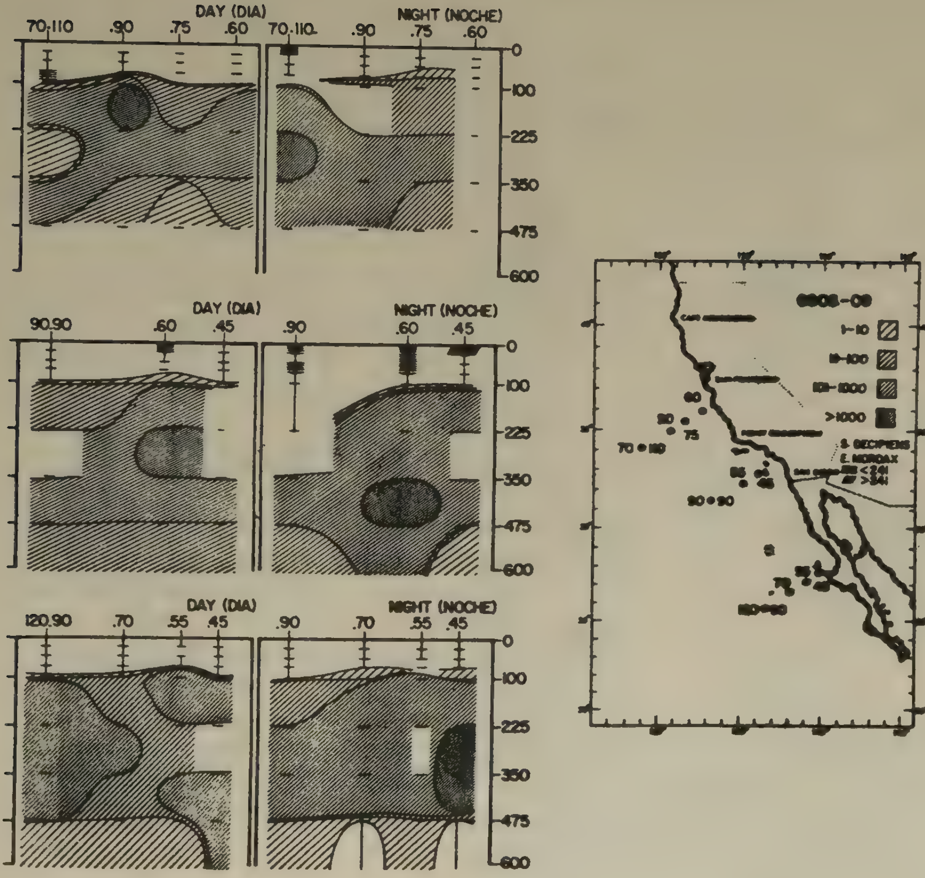

Fig. 3. Las surgencias en la región California-Baja California. Relaciones con el zooplancton y poblaciones de *E. mordax*.

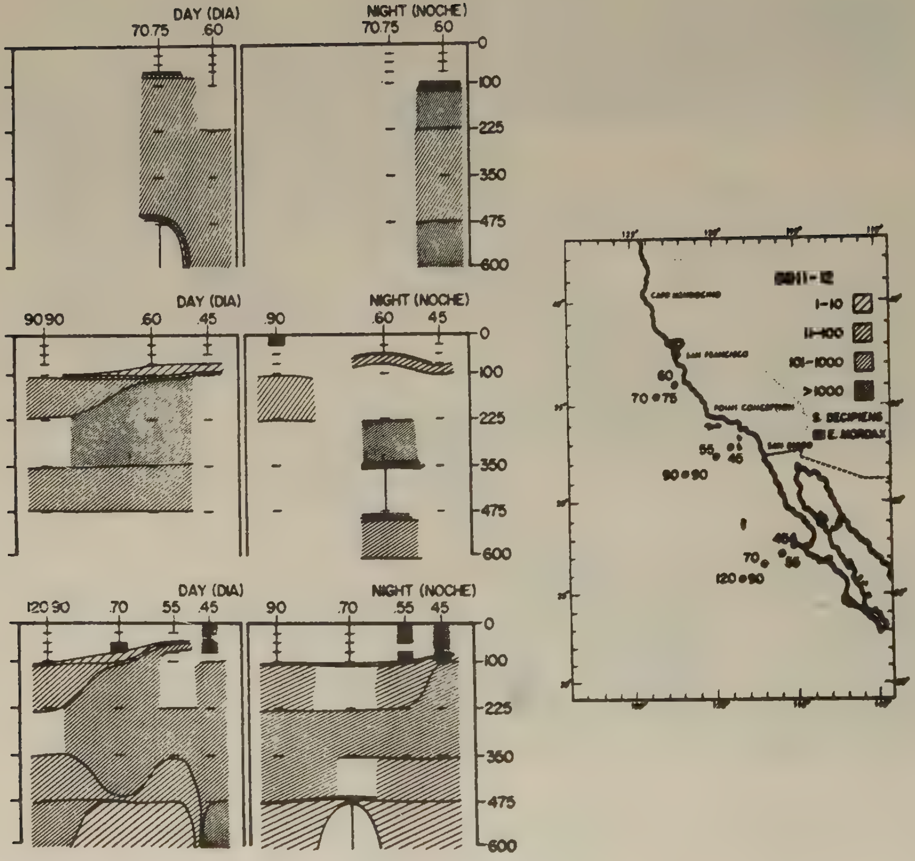

Fig. 4. Las surgencias en la región de California-Baja California. Relaciones con el zooplancton y poblaciones de *E. mordax*.

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DISTRIBUCION BATIMETRICA DE ESPECIES DEL GENERO *LENSIA* EN AGUAS DE CALIFORNIA Y BAJA CALIFORNIA

(DIPHYIDAE, SIPHONOPHORAE, COELENTERATA)

Angeles Alvariño*

RESUMEN

El género *Lensia* incluye 27 especies, de las cuales 16 se han observado durante 1969 en esta región, (*L. achilles*, *L. ajax*, *L. baryi*, *L. campanella*, *L. challengeri*, *L. conoidea*, *L. cossack*, *L. exeter*, *L. grimaldii*, *L. havock*, *L. hostile*, *L. hotspur*, *L. lelouveteau*, *L. multicristata*, *L. reticulata*, *L. subtilis*.

Las colecciones de plancton analizadas han sido obtenidas con redes bongo, de apertura y cierre automáticos, operando en 8 estratos de profundidad, desde los 600 m hasta 0 m. Las pescas se efectuaron consecutivamente, día y noche, en cada localidad y profundidad, y durante las cuatro estaciones del año.

Las especies de régimen templado, *L. challengeri*, *L. conoidea*, *L. hotspur*, *L. multicristata* aparecían abundante y frecuentemente distribuidas por la región. Las demás especies se observaron esparcidas en el tiempo y el espacio. Las especies tropicales eran más frecuentes en la zona más meridional de la región (frente a Baja California) avanzando en el invierno con la Corriente tropical hacia localidades más nórdicas.

L. challengeri y *L. multicristata* aparecían más abundantes en verano, y *L. conoidea*, *L. hotspur* en primavera, alcanzando mínimos en otoño e invierno.

Se señalan los estratos batimétricos habitados por *L. challengeri*, *L. conoidea*, *L. hotspur*, *L. multicristata*, día y noche y en relación con la estación del año. *L. campanella*, *L. cossack*, *L. exeter* y *L. subtilis* habitaban la zona epipelágica,

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mientras que las restantes ocho especies se encontraron en los estratos de la zona mesopelágica.

ABSTRACT

The genus *Lensia* includes 27 species, and 16 of those have been found off California and Baja California during the seasonal cruises of 1969. The species observed are: *L. achilles*, *L. ajax*, *L. baryi*, *L. campanella*, *L. challengeri*, *L. conoidea*, *L. cossack*, *L. exeter*, *L. grimaldii*, *L. havock*, *L. hostile*, *L. hotspur*, *L. lelouveteau*, *L. multicristata*, *L. reticulata*, *L. subtilis*.

The plankton collections analyzed had been obtained with paired open-closing bongo nets, with hauls at eight depth strata intervals from 600 m to 0 m. Hauls were made at about noon and midnight at each location and depth during the seasonal cruises.

Temperate species *L. challengeri*, *L. conoidea*, *L. hotspur*, *L. multicristata*, appeared abundant and frequently in those regions. The rest of the species of *Lensia* were scattered distributed. Tropical species were more often observed at the southern part of the surveyed region (off Baja California) progressing northward with the tropical current in winter.

L. challengeri and *L. multicristata* appeared more abundant in summer, and *L. conoidea* and *L. hotspur* in spring, and these four species reached minima in fall and winter.

The bathymetric layers inhabited day/night and seasonally by *L. challengeri*, *L. conoidea*, *L. hotspur* and *L. multicristata* are discussed. *L. campanella*, *L. cossack*, *L. exeter* and *L. subtilis* inhabit the epipelagic layers, while the other sight species were only observed at the mesopelagic domain.

INTRODUCCION

Se conocen en la actualidad 27 especies del género *Lensia*, de las cuales 16 han sido observadas durante 1969 en aguas de California y Baja California. Entre estas especies se encuentran representantes de aguas frías, templadas y cálidas. Los datos que hasta la fecha se tienen sobre la distribución de las especies del género *Lensia* aparecen recopilados en Alvariño (1971, 1981), Alvariño y Wojtan 1984. Alvariño (1967) informa sobre la distribución batimétrica de Sifonóforos en aguas de California.

Mediante el estudio de las colecciones de 1969 obtenidas con redes de apertura y cierre automáticos, a varios estratos de profundidad, día y noche, durante las cuatro estaciones del año, se ha podido determinar con precisión la distribución batimétrica de las especies y sus variaciones en relación con la época del año y el período del día.

METODOS

Las muestras de plancton estudiadas corresponden a las colecciones en las regiones de California y Baja California, en estaciones distribuidas en varias series frente a Monterrey y San Diego (California), y a la altura de Punta Eugenia (Baja California). Se utilizaron en estas colectas, redes pares bongo, de apertura y cierre automáticos, y malla de 505µ y 303µ.

Las colecciones de plancton se obtuvieron en las cuatro estaciones del año 1969, con cruceros en invierno (Febrero-Marzo, 6902-03), primavera (Mayo-Junio, 6905-06), verano (Agosto-Septiembre, 6908-09), otoño (Noviembre-Diciembre, 6911-12). Las figuras presentan la distribución de las localidades ocupadas.

Los estratos de profundidad ocupados en cada localidad se extendían desde los 600 m hasta la superficie oceánica, distribuidos entre los 600-475m, 475-350m, 350-225m, 225-100m, 100-75m, 75-50m, 50-25m, 25-0m. En cada localidad y estrato batimétrico se tomaron día y noche muestras de plancton, de modo que así se han podido obtener datos de la misma localidad y profundidad para el día y la noche, con un intervalo mínimo de unas doce horas.

En cada lance se filtraron 1000 m^3 de agua, cantidad calibrada y regulada mediante la velocidad de arrastre y la amplitud del estrato abarcado por el arrastre.

Se ha analizado la totalidad de la muestra de plancton recolectada en cada caso, contando los ejemplares para cada una de las especies, y efectuando las estimaciones convenientes, para que los datos resultasen comparables.

Hay que tener en cuenta la diferencia de velocidad de captura y amplitud del estrato abarcado por la muestra, ya que en los estratos de 100 a 0 m los lances abarcan únicamente 25 m, mientras que por debajo de los 100 m los arrastres abarcan 125 m, de modo que la velocidad en los estratos profundos viene a ser cinco veces mayor. En cada intervalo de 25 m, por debajo de los 100 m de profundidad, la cantidad de agua filtrada resulta ser de 225 m^3 apróximadamente.

Las estimaciones se obtienen mediante la fórmula:

$$N = \frac{n\ (\text{profundidad de apertura-profundidad de cierre})}{25}$$

N= cantidad total de ejemplares calculados

n= número de ejemplares en el par de redes

Para obtener datos cuantitativos en el estudio de los Sifonóforos, existe alguna dificultad, ya que constan de varias partes que se desprenden fácilmente durante las operaciones de captura. La familia Diphyidae, que incluye el género *Lensia*, no ofrece dificultad, ya que la fase poligástrica se caracteriza por tener dos nectoforos, superior e inferior. Así, en cada muestra de plancton se anota el número de nectoforos superiores e inferiores que aparecen para cada una de las especies, y entonces, la cantidad que se adjudica a la especie se basa en el número mayor que se obtenga, ya sea del nectoforo superior o del inferior.

DISTRIBUCION DE LAS ESPECIES DEL GENERO LENSIA

Entre las 16 especies del género *Lensia* obtenidas en aguas de California y Baja California, cuatro especies aparecen abundante y frecuentemente distribuidas por estas regiones, *Lensia challengeri* Totton, 1954, *L. conoidea* Kefferstein y Ehlers 1861, *L. hotspur*, Totton, 1954, *L. multicristata* Moser, 1925. Estas especies son típicas de aguas templadas. Las doce especies restantes se observaron esparcidas de forma errátil, tanto en el tiempo como en el espacio, y se trata de sifonóforos de aguas frías, cálidas o templadas.

DISTRIBUCION DE *LENSIA CHALLENGERI*

Se trata de una especie abundante en el Indo-Pacífico, particularmente en el Pacífico oriental. Así, es la especie de *Lensia* más frecuente y abundante en California y Baja California. Se presentaba con mayor abundancia y frecuencia en el invierno (Tabla 1) y con mínima frecuencia en otoño. Sin embargo, el número de ejemplares alcanzaba máximos en verano y mínimos en otoño. *L. challengeri* aparecía en invierno con el mismo promedio de abundancia en las colecciones diurnas y nocturnas, en primavera y verano el promedio de abundancia era más elevado en las capturas nocturnas que diurnas, y en el otoño resultaban promedios mayores para los arrastres diurnos. Las frecuencias aparecían con un valor ligeramente más elevado por la noche, en primavera, verano y otoño, y en las colecciones diurnas del invierno.

La distribución batimétrica de *L. challengeri* abarcaba en el invierno desde la superficie hasta los 350 m de profundidad. En primavera su distribución se extendía por todos los estratos ocupados desde 0 m hasta 600 m de profundidad, con máximos entre los 50-100 m. En el verano esta especie no aparecía hasta los 75 m de profundidad, con máximos por debajo de los 100 m, principalmente en las colectas nocturnas. La densidad de población es baja en el otoño, presentándose a más de 50 m de profundidad. (Figs. 1, 2, 3, 4).

En general no se ha observado diferencia en las colectas diurnas y nocturnas para señalar desplazamientos verticales en relación con el período del día.

DISTRIBUCION DE *LENSIA CONOIDEA*

Es una especie abundante en todos los océanos. En las regiones de California y Baja California es la segunda en abundancia para el género *Lensia*.

L. conoidea aparecía con máximos de frecuencia en verano (24%) para colectas combinadas de día y noche, y mínimos en invierno (7%), mientras que los promedios de abundancia resultaban con máximos en primavera, seguidos en orden decreciente, por el verano, invierno y otoño. En el invierno aparecía distribuida desde los 25 m hasta los 350 m de profundidad (máximo nivel batial alcanzado por las redes). En la primavera y verano se extendía de los 75 m hasta los 600 m de profundidad, con máximos a los 225-350 m, y en el otoño de los 100 m hasta los 600 m con máximo a los 100-225 m de profundidad.

L. conoidea se observó más abundante en las colecciones nocturnas de primavera y otoño, con una frecuencia mayor para las colecciones nocturnas del verano, aunque el promedio de abundancia resultaba más elevado para colectas diurnas, y durante el invierno los máximos de frecuencia y abundancia pertenecían a colecciones diurnas, estando ausente de las nocturnas. Tabla 2.

No se ha observado variación en la distribución vertical con relación al período del día, es decir, que las poblaciones se presentasen más cerca de la superficie oceánica durante la noche o el día. (Figs. 1, 2, 3, 4).

DISTRIBUCION DE *LENSIA HOTSPUR*

Esta especie es abundante en las regiones de California y Baja California. El máximo de frecuencia correspondía al verano y el promedio de abundancia a la primavera, seguido en orden decreciente para ambos parámetros,por el invierno y otoño. Tabla 3. *L. hotspur* se presentaba irregularmente esparcida por los estratos batiales, y las frecuencias y promedios están asimismo irregularmente distribuidos en los períodos del día.

En invierno la frecuencia era máxima (11%) para las colecciones diurnas, y el promedio de abundancia resultaba sensiblemente igual para ambos períodos del día. En la primavera la frecuencia era ligeramente mayor para las muestras nocturnas, - mientras que la mayor abundancia correspondía a las diurnas. En verano la frecuencia era más elevada para las colecciones - diurnas y el promedio de abundancia en las nocturnas, mientras que en otoño la frecuencia resultaba ligeramente más elevada para las pescas nocturnas.

La fluctuación batimétrica en la distribución de *L. hotspur*, con el período del día resultaba similar para la primavera y otoño, alcanzando en invierno y verano estratos más cercanos a la superficie oceánica durante el día. (Figs. 1, 2 3, 4).

DISTRIBUCION DE *LENSIA MULTICRISTATA*

Es una especie común al Atlántico, Indico y Pacífico. En la zona de California y Baja California aparecía en 1969 con mayor abundancia en el verano, seguido en orden decreciente por el otoño y primavera, y mínimos en el invierno, cuando se extendía desde los 50 m hasta los 225 m de profundidad. En primavera, verano y otoño se observó desde los 100 m hasta los 600 m, con máximos a los 225-350 m. (Tabla 4). *L. multicristata* aparecía con mayor frecuencia y abundancia en las pescas nocturnas del verano y otoño, con mayor frecuencia durante la noche en la primavera, aún cuando el promedio de abundancia resultaba más elevado de día, y en el invierno la frecuencia y promedio de abundancia resultaban más elevados de día.

La distribución vertical, es decir, la profundidad mínima abarcada por las poblaciones de *L. multicristata* con respecto al período del día, era similar para ambos períodos. (Figs. 1, 2, 3, 4).

DISTRIBUCION DE LAS DEMAS ESPECIES DEL GENERO *LENSIA*

Las restantes doce especies del género *Lensia* aparecían con distribución errátil, Tabla 5. Se trata de una mezcla de especies de aguas frías, templadas y cálidas, esparcidas por el ámbito oceánico con poblaciones de escasa densidad.

Las especies consideradas hasta la fecha frecuentes en las regiones tropicales son: *L. ajax*, Totton, 1941, *L. campanella* Moser, 1925, *L. cossack* Totton, 1941, *L. exeter* Totton, 1941, *L. grimaldii* Leloup, 1933, *L. havock* Totton, 1941.

Lensia campanella habitaba las localidades más meridionales, frente a Baja California, ocupando los estratos más cercanos a la superficie oceánica, desde los 0 m a los 50 m de profundidad. (Fig. 5). *Lensia cossack* se observó en el otoño frente a Monterrey, a los 25-50 m(Fig. 6). *L. exeter* aparecía frente a Baja California, a los 75-100, de profundidad. (Fig. 7).

L. ajax, *L. grimaldii*, *L. havock*, *L. hostile*, Totton, 1941, *L. lelouveteau* Totton, 1941, *L. reticulata* Totton 1954, se observaron (Figs. 5, 6, 7) esparcidas en los estratos de los 225 m a los 600 m de profundidad. *L. grimaldii* y *L. ajax* ocupaban localidades más oceánicas, *L. hostile* más cercanas al continente (frente a Monterrey, San Diego y Punta Eugenia), *L. havock* y *L. lelouveteau* en aguas de San Diego y Punta Eugenia, y *L. reticulata* en la región de las Islas de California meridional.

Lensia achilles Totton, 1941, y *L. subtilis* Chun 1886 son típicas de aguas templadas. La primera aparecía en los 475-600 m de profundidad, mientras que *L. subtilis* se observó en invierno y primavera a los 0-25 m, y en otoño a los 100-225 m de profundidad. (Tabla 5, Figs. 5, 7).

Lensia baryi Totton 1965, es una especie típica del Pacífico canadiense, y se observó durante el otoño en las localidades frente a Monterrey, a los 225-475 m de profundidad. (Tabla 5, Fig. 5).

En los mapas se incluye la distribución de las especies raras (Figs. 5, 6, 7) combinando todos los datos correspondientes a los cruceros realizados durante el año 1969 en aguas de California y Baja California.

Con este estudio se obtienen determinaciones nuevas de especies de *Lensia* para la región de California y Baja California, como sigue: *L. baryi*, *L. campanella*, *L. cossack*, *L. exeter* y *L. subtilis*. Las demás especies de *Lensia* aquí mencionadas han sido observadas previamente (Alvariño, 1971) en estas regiones.

TABLA 1. DISTRIBUCION DE *Lensia challengeri* EN CALIFORNIA Y BAJA CALIFORNIA, 1969.

Est. / Prof. m	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Promedio total		% Frecuencia		
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	Dia	Noche	D	N	D/N
6902-03																											
25- 0	0	0	0	17	-	-	-	-	0	0	0	0	-	-	0	0	19	0	12	0	0	0	3	2			
50- 25	-	0	1	0	-	-	-	-	0	0	18	0	-	-	0	0	-	0	0	18	0	0	3	2			
75- 50	0	-	4	-	-	-	-	-	5	50	0	18	-	-	0	0	-	0	0	56	-	-	1	24			
100- 75	4	-	0	-	-	-	-	-	8	4	27+5*	9	-	-	8	9	1	0	10	43	0	0	7	7			
225-100	-	-	0	-	-	-	-	-	92	-	81	-	-	-	78	-	-	1	-	100	0	0	50	33			
350-225	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	4	-			
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
																							Total no. indiv. =	701	40%	36%	38%
6905-06																											
25- 0	0	1	0	0	0	0	0	0	-	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0.2			
50- 25	0	1	0	0	0	0	-	0	-	0	0	0	0	0	83	0	0	0	0	0	-	0	10	0			
75- 50	70	18	8	50	1	0	-	0	-	42	18	20	0	0	92	56	0	61	0	0	0	0	21	22			
100- 75	9	6	33	10	4	1	-	0	-	93	30	16	-	0	76	24	-	172	-	0	-	0	32	29			
225-100	0	0	0	10	0	0	0	0	-	240	45	15	-	80	10	5	10	210	0	0	-	0	8	51			
350-225	-	0	0	0	0	0	0	0	-	25	135	0	-	-	40	350	0	0	0	-	-	0	25	41			
475-350	0	0	0	0	0	0	0	0	-	0	0	0	-	0	215	0	0	0	0	0	0	0	23	0			
600-475	0	0	0	0	0	0	-	0	-	0	0	0	-	0	0	25	0	-	0	25	-	0	0	5			
																							Total no. indiv. =	2457	27%	30%	29%
6908-09																											
25- 0	-	-	-	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0			
75- 50	-	-	-	16	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	1			
100- 75	-	-	-	2	0	0	0	-	0	18	0	1	0	0	30	0	16	0	0	0	0	0	5	2			
225-100	50	-	0	5	0	-	0	0	-	85	25	10	0	0	65	3010	30	20	230	10	0	0	40	348			
250-225	0	-	20	0	0	0	165	0	-	-	10	0	-	-	-	1370	0	-	100	0	0	0	36	195			
475-350	0	-	0	0	0	0	0	0	0	0	0	0	0	0	330	2165	0	0	0	0	0	5	30	217			
600-475	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2275	0	0	0	0	0	0	0	325			
																							Total no. indiv. =	10064	18%	19%	19%
6911-12																											
25- 0	0	0	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	0	0	0	-	-	-	-	-	0	-	0	0	0	-	0	0	-	0	0	0	0	0	0	0			
75- 50	0	0	0	-	-	-	-	-	-	-	0	0	0	-	1	10	6	-	60	16	0	0	8	5			
100- 75	0	-	0	-	-	-	-	-	1	2	0	-	-	-	-	4	-	3	5	0	0	0	1	1			
225-100	-	10	0	-	-	-	-	-	-	-	0	-	0	0	15	0	-	30	75	-	0	0	15	8			
350-225	0	0	0	-	-	-	-	-	-	-	0	0	-	-	0	5	0	0	0	0	-	0	0	0.8			
475-350	0	0	0	-	-	-	-	-	-	-	0	0	0	-	0	0	0	0	0	-	0	0	0	0			
600-475	0	5	0	-	-	-	-	-	-	-	-	0	-	-	-	0	0	0	0	0	0	0	0	0.8			
																							Total no. indiv. =	248	12%	19%	15%
																							Gran total =	13470	Total % freq. = 25%		

D= Colecciones diurnas

N= Colecciones nocturnas

*= eudoxias

TABLA 2. DISTRIBUCION DE *Lensia conoidea* EN CALIFORNIA Y BAJA CALIFORNIA, 1969.

Est. / Prof. m	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Promedio total		% Frecuencia		
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	Dia	Noche	D	N	D/N
6902-03																											
25- 0	0	0	0	0	-	-	-	-	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0			
50- 25	-	0	0	0	-	-	-	-	18	0	0	0	-	-	0	0	-	0	0	0	0	0	3	0			
75- 50	0	-	74	-	-	-	-	-	0	2	0	0	-	-	0	0	-	0	0	0	-	-	12	0.4			
100- 75	0	-	0	-	-	-	-	-	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0			
225-100	-	-	0	-	-	-	-	-	11	-	82	-	-	-	0	-	-	0	-	0	0	0	18	0			
350-225	-	-	505	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	252	-			
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
																					Total no. indiv. =			692	14 %	0 %	7 %
6905-06																											
25- 0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0			
75- 50	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
100- 75	0	9	41	0	0	0	-	0	-	0	0	0	-	0	0	0	-	0	-	0	-	0	8	0			
225-100	40	475	260	141	0	0	0	0	-	215	0	30	-	0	0	0	0	0	0	0	-	0	37	78			
350-225	-	620	470	75	1335	470	5	0	-	90	0	295	-	-	0	0	0	0	0	-	-	0	258	161			
475-350	5	0	10	0	50	5	130	0	-	0	315	0	-	1410	0	0	0	0	0	5	0	0	56	129			
600-475	0	5	0	10	0	0	-	0	-	0	0	0	-	5	0	0	0	-	0	5	-	0	0	2			
																					Total no. indiv. =			6526	17 %	20 %	18 %
6908-09																											
25- 0	-	-	-	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0			
75- 50	-	-	-	0	0	1	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0			
100- 75	-	-	-	164	0	14	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19			
225-100	70	-	120	120	350	-	0	50	-	130	0	55	0	0	0	0	0	0	0	0	0	0	54	50			
350-225	15	-	50	40	630	320	90	130	-	-	90	45	-	-	-	0	5	-	0	0	0	5	110	90			
475-350	0	-	0	0	0	5	95	5	20	0	55	80	10	10	0	0	20	0	0	0	0	5	18	10			
600-475	0	-	-	-	-	-	-	-	10	0	0	0	0	0	10	5	0	0	0	0	0	0	2	0.7			
																					Total no. indiv. =			2824	23 %	25 %	24 %
6911-12																											
25- 0	0	0	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	0	0	0	-	-	-	-	-	0	-	0	0	0	-	0	0	-	0	0	0	0	0	0	0			
75- 50	0	0	0	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	0	0			
100- 75	0	-	1	-	-	-	-	-	0	0	0	-	-	-	-	0	-	0	0	0	0	0	0	0			
225-100	-	415	270	-	-	-	-	-	-	-	0	-	0	0	0	0	-	0	0	-	0	0	45	83			
350-225	0	35	0	-	-	-	-	-	-	-	25	100	-	-	0	5	5	0	0	0	-	0	5	23			
475-350	0	0	0	-	-	-	-	-	-	-	30	0	0	-	0	0	0	0	0	-	0	0	3	0			
600-475	240	175	0	-	-	-	-	-	-	-	-	20	-	-	0	0	0	0	0	0	0	0	40	32			
																					Total no. indiv. =			1321	10 %	13 %	11 %
																							Gran total =	11363	Total % frec.=17.3%		

D= Colecciones diurnas

N= Colecciones nocturnas

TABLA 3. DISTRIBUCION DE *Lensia multicristata* EN CALIFORNIA Y BAJA CALIFORNIA, 1969.

Est. / Prof. m	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Promedio total		% Frecuencia		
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	Dia	Noche	D	N	D/N
6902-03																											
25- 0	0	0	0	0	-	-	-	-	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0			
50- 25	-	0	0	0	-	-	-	-	0	0	0	0	-	-	0	0	-	0	0	0	0	0	0	0			
75- 50	0	-	0	-	-	-	-	-	6	0	0	0	-	-	0	0	-	0	0	0	-	-	1	0			
100- 75	26	-	0	-	-	-	-	-	0	16	0	0	-	-	0	0	0	0	0	0	0	0	6	2			
225-100	-	-	170	-	-	-	-	-	1	-	153	-	-	-	0	-	-	0	-	8	0	0	65	3			
350-225	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-			
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
																							Total no. indiv. =	380	14 %	6 %	10 %
6905-06																											
25- 0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0			
75- 50	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
100- 75	0	5	0	0	0	0	-	0	-	0	0	0	-	0	0	0	-	0	-	0	-	0	0	0			
225-100	0	0	0	0	80	0	0	5	-	5	5	0	-	0	0	95	0	0	0	0	-	0	10	9			
350-225	-	85	0	40	335	135	0	70	-	170	315	320	-	-	0	0	90	0	0	-	-	0	105	87			
475-350	0	5	0	0	0	0	0	5	-	0	85	0	-	0	0	5	0	5	10	0	0	10	10	2			
600-475	0	0	0	0	0	0	-	5	-	0	0	0	-	65	5	0	0	-	10	20	-	0	2	9			
																							Total no. indiv. =	1945	14 %	20 %	17 %
6908-09																											
25- 0	-	-	-	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	1	0	0			
75- 50	-	-	-	0	1	2	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0			
100- 75	-	-	-	8	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1			
225-100	15	-	0	5	90	-	0	40	-	15	15	25	0	0	0	0	0	10	0	5	0	0	12	11			
350-225	155	-	50	75	265	55	240	165	-	-	25	190	-	-	-	5	0	-	5	10	0	20	92	74			
475-350	5	-	0	0	10	5	0	20	5	0	15	150	25	40	0	0	5	10	0	25	5	0	6	25			
600-475	0	-	-	-	-	-	-	-	0	0	0	10	10	10	0	0	0	5	0	0	0	0	1	3			
																							Total no. indiv. =	1851	37%	36%	32%
6911-12																											
25- 0	0	0	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	0	0	0	-	-	-	-	-	0	-	0	0	0	-	0	0	-	0	0	0	0	0	0	0			
75- 50	0	0	0	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	0	0			
100- 75	0	-	0	-	-	-	-	-	0	0	0	-	-	-	-	0	-	0	0	0	0	0	0	0			
225-100	-	80	175	-	-	-	-	-	-	-	10	-	0	5	0	0	-	0	0	-	0	0	30	19			
350-225	0	0	0	-	-	-	-	-	-	-	15	75	-	-	73	35	35	85	0	80	-	300	10	109			
475-350	0	0	5	-	-	-	-	-	-	-	0	0	10	-	75	5	10	5	5	-	0	0	12	2			
600-475	60	90	0	-	-	-	-	-	-	-	-	5	-	-	0	0	0	0	0	0	5	0	10	15			
																							Total no. indiv. =	1265	21%	32%	23%
																							Gran total =	5441	Total % frec. = 22%		

D= Colecciones diurnas

N= Colecciones nocturnas

TABLA 4. DISTRIBUCION DE *Lensia hotspur* EN CALIFORNIA Y BAJA CALIFORNIA, 1969.

Est. / Prof. m	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Promedio total		% Frecuencia		
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	Dia	Noche	D	N	D/N
6902-03																											
25- 0	0	0	0	0	-	-	-	-	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0			
50- 25	-	0	0	0	-	-	-	-	0	0	0	0	-	-	0	0	-	0	6	0	0	0	1	0			
75- 50	0	-	19	-	-	-	-	-	0	0	0	0	-	-	0	0	-	0	0	0	-	-	3	0			
100- 75	8	-	0	-	-	-	-	-	0	0	0	0	-	-	0	0	0	0	0	0	0	0	1	0			
225-100	-	-	0	-	-	-	-	-	1	-	0	-	-	-	0	-	-	0	-	33	21	0	4	8			
350-225	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-			
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
																				Total no. indiv. =				88	11 %	3 %	7 %
6905-06																											
25- 0	0	0	0	0	0	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	0	1	0	0	0	1	-	0	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0			
75- 50	16	0	0	8	0	9	-	8	-	0	0	0	0	0	1	0	0	0	0	0	0	0	2	2			
100- 75	8	0	17	0	61	9	-	16	-	1	0	0	-	0	0	4	-	0	-	0	-	0	17	2			
225-100	0	0	0	0	0	0	1015	0	-	0	0	0	-	10	0	0	0	0	0	0	-	0	126	1			
350-225	-	0	0	0	0	0	0	0	-	0	0	0	-	-	0	0	0	0	0	-	-	0	0	0			
475-350	0	0	0	0	0	0	0	0	-	0	0	0	-	5	0	0	0	0	0	0	0	0	0	0			
600-475	0	0	0	0	0	0	-	0	-	0	0	0	-	0	0	0	0	-	0	0	-	0	0	0			
																				Total no. indiv. =				1191	11%	14%	12%
6908-09																											
25- 0	-	-	-	0	-	0	-	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	2	0			
50- 25	-	-	-	0	90	0	62	2	0	0	2	30	0	0	0	30	-	0	0	0	60	0	24	6			
75- 50	-	-	-	0	0	3	45	92	0	0	-	1	1	0	0	0	0	-	0	0	0	0	5	10			
100- 75	-	-	-	0	2	0	2	-	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
225-100	5	-	0	5	0	-	10	260	-	0	0	0	0	0	5	0	5	0	0	5	0	0	2	30			
350-225	0	-	0	0	0	0	5	0	-	-	0	0	-	-	-	0	0	-	0	0	0	0	0	0			
475-350	0	-	0	0	0	0	0	0	0	0	0	0	0	0	75	375	0	0	0	0	0	0	6	37			
600-475	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
																				Total no. indiv. =				1189	23%	14%	18%
6911-12																											
25- 0	0	0	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
50- 25	0	0	0	-	-	-	-	-	0	-	0	0	0	-	0	0	-	0	0	0	0	0	0	0			
75- 50	0	0	2	-	-	-	-	-	-	-	0	15	16	-	0	0	0	-	0	0	0	0	2	3			
100- 75	0	-	24	-	-	-	-	-	0	4	0	-	-	-	-	0	-	0	0	0	0	0	4	1			
225-100	-	0	0	-	-	-	-	-	-	-	0	-	0	0	0	0	-	0	0	-	0	0	0	0			
350-225	0	0	0	-	-	-	-	-	-	-	0	0	-	-	0	0	0	0	0	0	-	0	0	0			
475-350	0	0	0	-	-	-	-	-	-	-	0	0	0	-	0	5	0	0	0	-	0	0	0	1			
600-475	0	15	0	-	-	-	-	-	-	-	-	0	-	-	0	0	0	0	0	0	0	0	0	2			
																				Total no. indiv. =				81	5%	8%	6%
																					Gran total =			2549	Total % frec. = 12%		

D= Colecciones diurnas

N= Colecciones nocturnas

TABLA 5. DISTRIBUCION DE ESPECIES DE *Lensia* POCO ABUNDANTE.

CRUCERO	ESPECIES	LOCALIDAD	PROF. (m)	No. de ejemplares DIA	NOCHE
6902-03	*Lensia campanella*	120.90	15- 0	1	
	L. exeter	120.70	100- 75	4	
	L. grimaldii	120.90	200-150	16	
	L. subtilis	120.55	15- 0	36	
6905-06	*L. achilles*	70.60	600.475	10	
	L. ajax	70.110	475.350		5
	L. campanella	120.90	25- 0	1	
	L. grimaldii	70.90	475.350		5
	L. havock	90.45	475.350		10
	L. hostile	70.60	350.225		5
		70.75	475-350		5
		90.45	600.475		5
	L. lelouveteau	90.45	350.225		5
	L. subtilis	70.110	25- 0	100	
6908-09	*L. achilles*	70.90	475-350		10
		90.90	600-475		5
	L. ajax	90.60	475-350		5
	L. campanella	120.70	50-25	15	
	L. grimaldii	70.110	350-225		10
		90.90	600-475		5
	L. havock	120.55	600-475	5	
	L. lelouveteau	120.45	225-100	5	
	L. reticulata	90.60	475-350		20
	L. achilles	70.75	475-350	10	
			600-475	10	
	L. ajax	90.60	600-475		75
	L. baryi	70.60	350-225	5	
			475-350	5	
	L. cossack	70.75	50- 25	1	
	L. havock	120.45	600-475	5	
		120.55	600-475	5	
		120.90	600-475		20
	L. hostile	120.70	600-475	5	
	L. subtilis	70.75	225-100	150	

BIBLIOGRAFIA

Alvariño, A. 1967. Bathymetric distribution of Chaetognatha, Siphonophorae, Medusae and Ctenophora off San Diego, California. Pacific Science, 21(4):274-285.

______________ 1969. Zoogeografía del Mar de Cortés: Quetognatos, Sifonóforos y Medusas. An. Inst. Biol. Univ. Nacl. Auton. México, Ser. Ciencia Mar. y Limnol. (1):11-54.

______________ 1971. Siphonophorae of the Pacific with a review of the World distribution. Bull. Scripps Inst. Oceanography, Univ. California La Jolla, California, 16:1-432.

______________ 1972. Zooplancton del Caribe, Golfo de México y regiones adyacentes del Pacífico. Mem. IV Nacl. Congreso Ocean. México. Pags. 223-247.

______________ 1974. Distribution of Siphonophores in the regions adjacent to the Suez and Panama Canals. Fish Bull. 72(2):527-546.

______________ 1976. El Zooplancton de la región de la América Central en el Pacífico. III Simposio Latinoaméricano sobre Oceanografía Biológica, El Salvador.

______________ 1977. El plancton del Pacífico Ecuatoriano. IV Simposio Latinoamericano sobre Oceanografía Biológica, Ecuador.

______________ 1981. Siphonophorae. Atlas del Zooplancton del Atlántico Sudoccidental. Pags. 383-441.

______________ y J.M. Wojtan 1984. Three new species of *Lensia*, and description of the eudoxia stages of *Lensia reticulata* and *Lensia lelouveteau* (Calycophorae: Siphonophorae). Proceedings of the Biological Society of Washington, 97(1):49-59.

Bigelow, H.B. 1911. The Siphonophorae. Rep. Sci. Res. Eastern Tropical Pacific Exped. ALBATROSS. Mem. Mus. Comp. Zool. Harvard, 38(2):173-401.

and M. Leslie 1939. Reconnaissance of the waters and plankton of Monterey Bay, July, 1928. Bull. Mus. Comp. Zool. Harvard, 70(5):429-581.

Pugh, P.R. 1974. The vertical distribution of the Siphonophores collected during the SOND Cruise, 1965. Journ. Mar. Biol. Assoc. U.K., 54:25-90.

Totton, A.K. 1941. New species of genus *Lensia* Totton 1932. Ann. Mag. Nat. Hist. Ser. 11, 8(45):145-168.

1965. A new species of *Lensia* (Siphonophora, Diphyidae) from the coastal waters of Vancouver, B.C., and its comparison with *Lensia achilles* Totton and another new species *Lensia cordata*. Ann. Mag. Nat. Hist. Ser. 13, 8(86):71-76.

and M.E. Bargmann 1965. A Synopsis of Siphonophora. British Museum of Natural History, I-VIII-230.

LEYENDAS DE LAS FIGURAS

Fig. 1. Distribución batimétrica de *Lensia challengeri, L. conoidea, L. hotspur, L. multicristata*. Los segmentos a la izquierda, debajo de la ilustración para cada especie, representan la zona batimétrica que habitan y su abundancia, según la escala que aparece en el mapa. Febrero-Marzo 1969.

Fig. 2. Distribución batimétrica de *Lensia challengeri, L. conoidea, L. hotspur, L. multicristata*. Los segmentos a la izquierda, debajo de la ilustración para cada especie, representan la zona batimétrica que habitan y su abundancia, según la escala que aparece en el mapa. Mayo-Junio, 1969.

Fig. 3. Distribución batimétrica de *Lensia challengeri*, *L. conoidea*, *L. hotspur*, *L. multicristata*. Los segmentos de la izquierda, debajo de la ilustración para cada especie, representan la zona batimétrica que habitan y su abundancia, según la escala que aparece en el mapa. Agosto-Septiembre, 1969.

Fig. 4. Distribución batimétrica de *Lensia challengeri*, *L. conoidea*, *L. hotspur*, *L. multicristata*. Los segmentos a la izquierda, debajo de la ilustración para cada especie, representan la zona batimétrica que habitan y su abundancia, según la escala que aparece en el mapa. Noviembre-Diciembre, 1969.

Fig. 5. Distribución de *Lensia baryi*, *L. campanella*, *L. lelouveteau*, *L. subtilis*, combinando todos los datos correspondientes a las cuatro estaciones del año 1969.

Fig. 6. Distribución de *Lensia cossack*, *L. grimaldii*, *L. hostile*, *L. reticulata*, combinando todos los datos correspondientes a las cuatro estaciones del año 1969.

Fig. 7. Distribución de *Lensia achilles*, *L. ajax*, *L. exeter*, *L. havock*, combinando todos los datos correspondientes a las cuatro estaciones del año 1969.

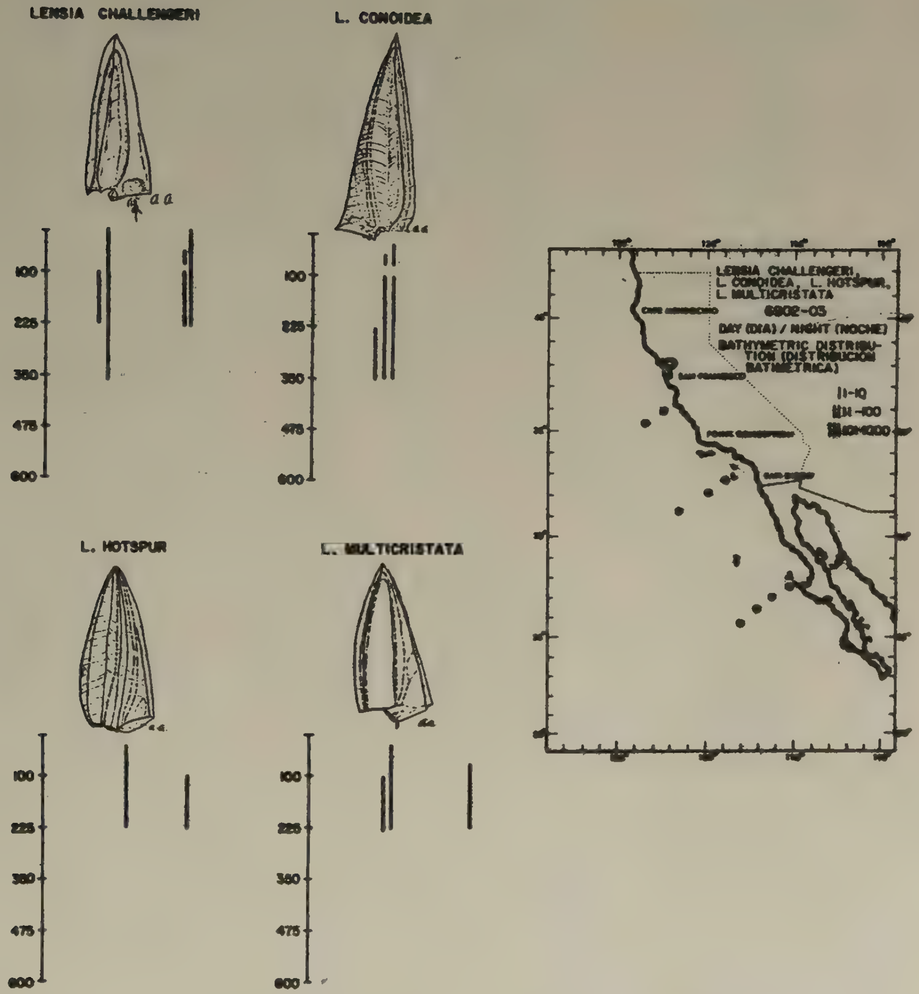

Fig. 1. Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California (Diphyidae, Siphonophorae, Coelenterata).

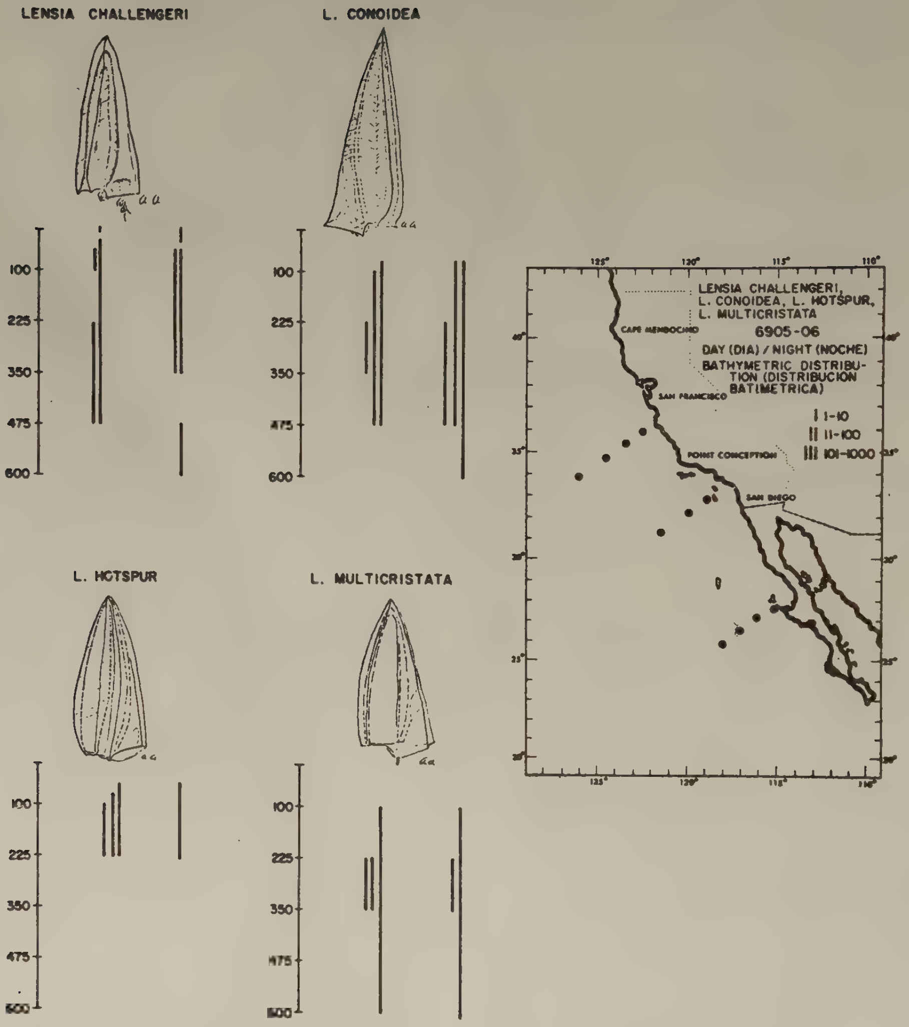

Fig. 2. Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California. (Diphyidae, Siphonophorae, Coelenterata).

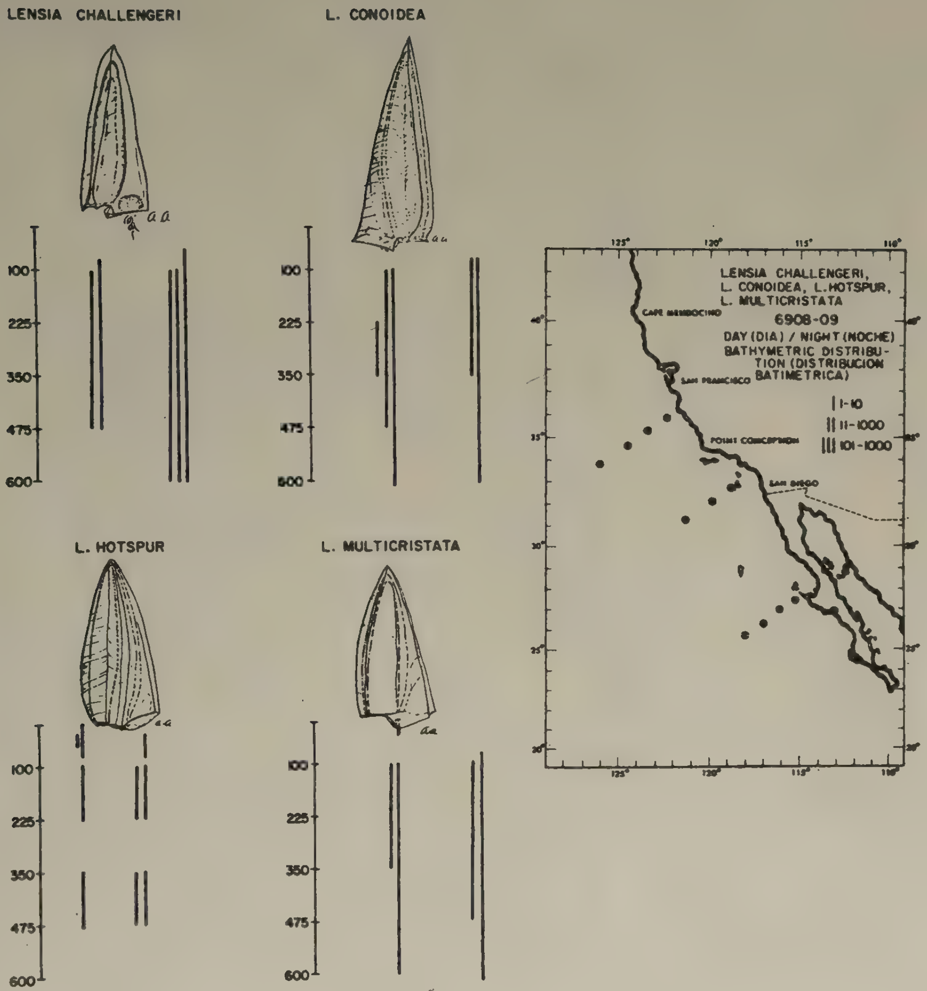

Fig. 3. Distribución batimétrica de especies del género *lensia* en aguas de California y Baja California (Diphyidae, Siphonophorae, Coelenterata).

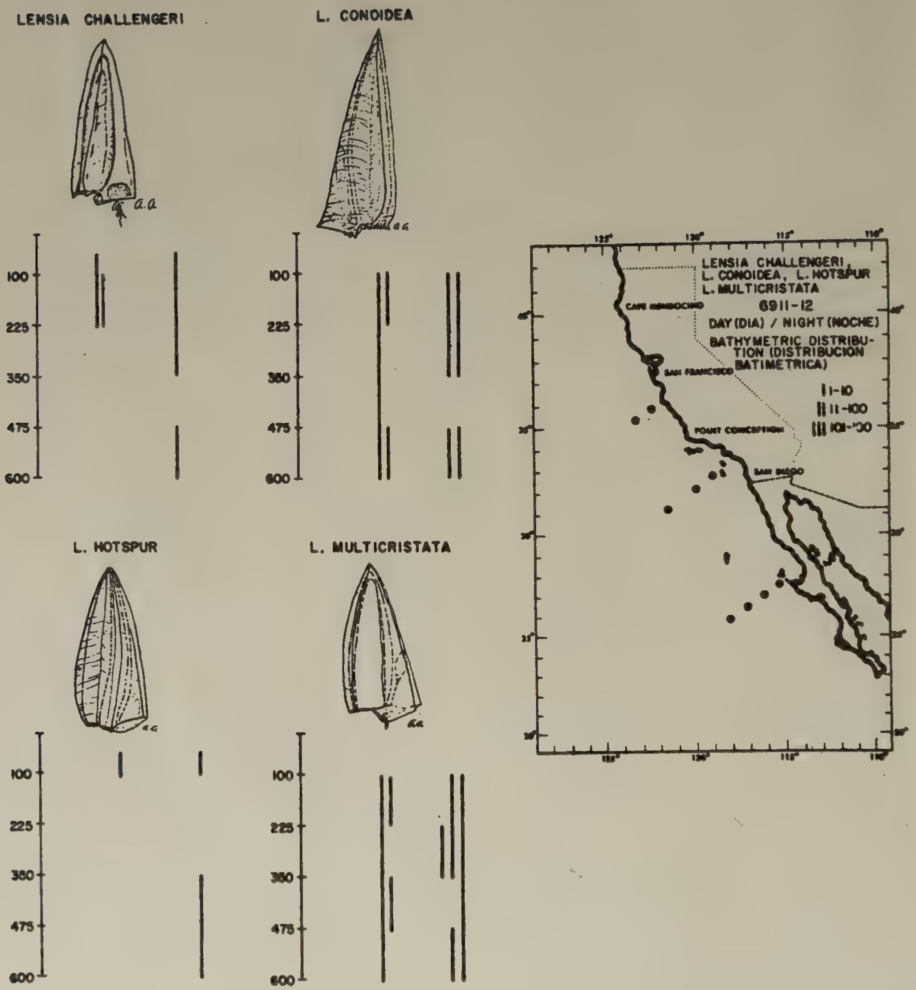

Fig. 4. Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California (Diphyidae, Siphonophorae, Coelenterata).

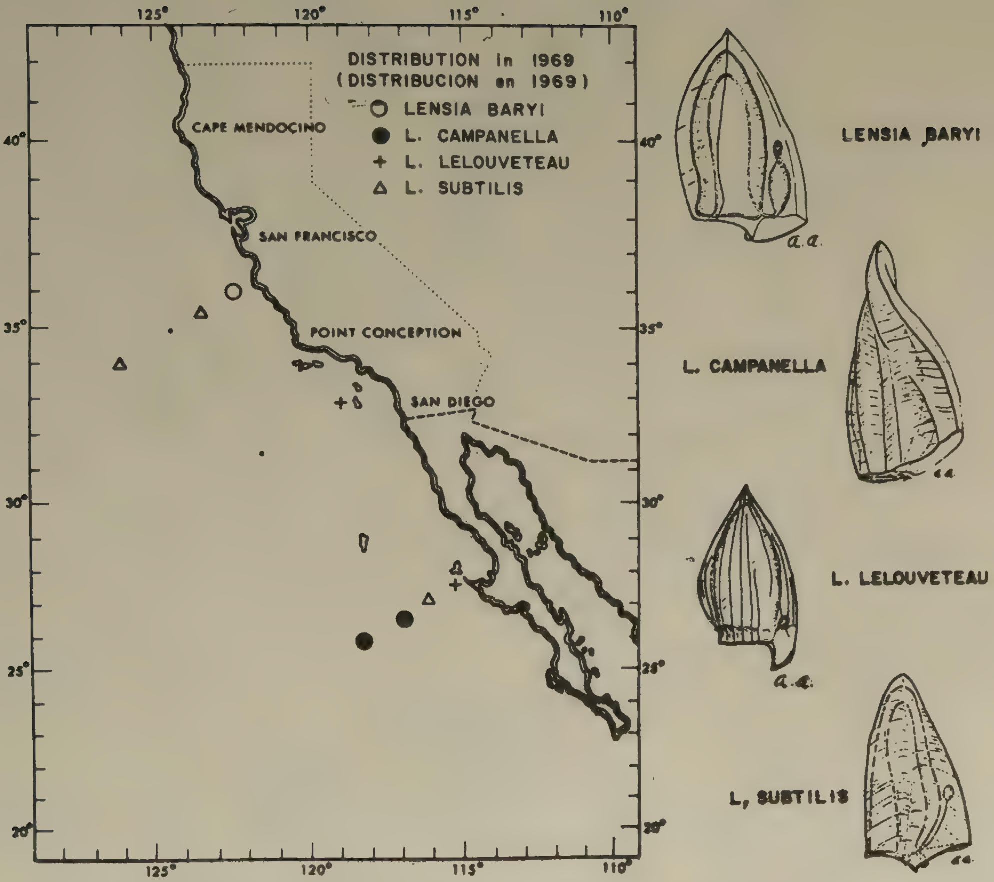
125°
120°
115°
110°
DISTRIBUTION in 1969
(DISTRIBUCION en 1969)
○ LENSIA BARYI
● L. CAMPANELLA
+ L. LELOUVETEAU
△ L. SUBTILIS
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
40°
35°
30°
25°
20°
LENSIA BARYI
a.a.
L. CAMPANELLA
a.a.
L. LELOUVETEAU
a.a.
L, SUBTILIS
a.a.

Fig. 5. Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California (Diphyidae, Siphonophorae, Coelenterata).

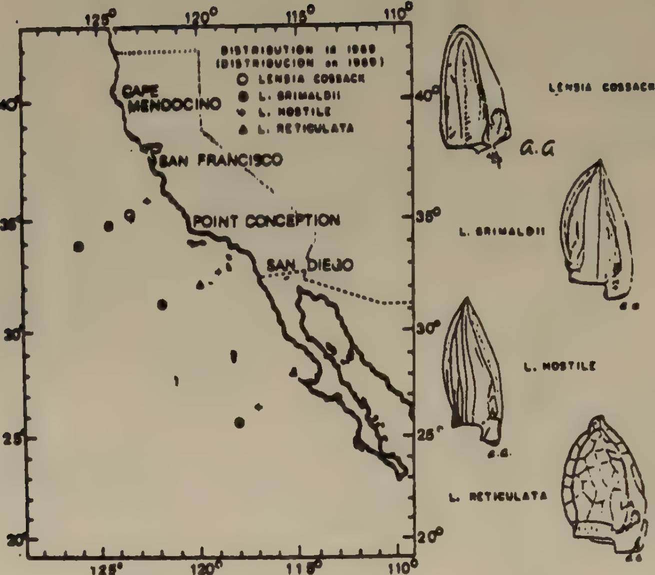
125°
120°
115°
110°
DISTRIBUTION in 1969
(DISTRIBUCION en 1969)
○ LENSIA COSSACK
● L. GRIMALDII
✦ L. HOSTILE
▲ L. RETICULATA
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
40°
35°
30°
25°
20°
LENSIA COSSACK
L. GRIMALDII
L. HOSTILE
L. RETICULATA
G.G

Fig. 6. Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California. (Diphyidae, Siphonophorae, Coelenterata).

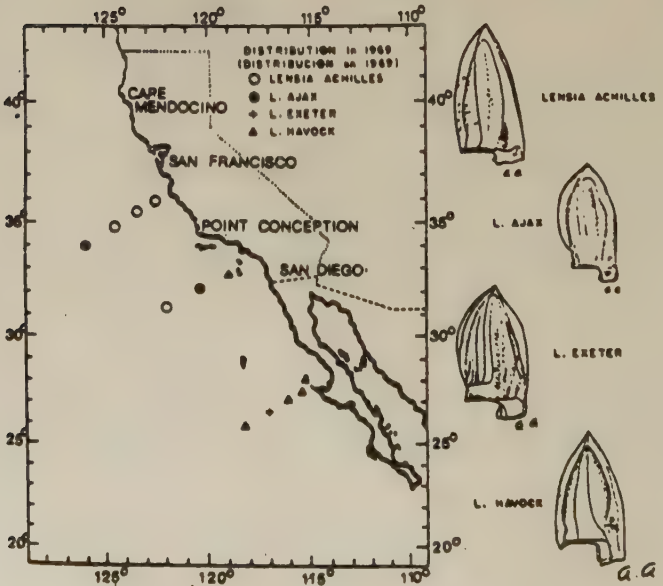
125°
120°
115°
110°
DISTRIBUTION in 1969
(DISTRIBUCION en 1969)
○ LENSIA ACHILLES
● L. AJAX
✦ L. EXETER
▲ L. HAVOCK
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
40°
35°
30°
25°
20°
LENSIA ACHILLES
L. AJAX
L. EXETER
L. HAVOCK
G.G

Fig. 7. Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California (Diphyidae, Siphonophorae, Coelenterata).

8504

FOOD HABITS OF BAIT-CAUGHT SKIPJACK TUNA, *KATSUWONUS PELAMIS*, FROM THE SOUTHWESTERN ATLANTIC OCEAN

LISA ANKENBRANDT[1]

ABSTRACT

Stomach contents of skipjack tuna captured in 1981-82 by live pole-and-line vessels off the southern coast of Brazil were analyzed for the presence of larval and juvenile skipjack tuna. The percentage frequency of occurrence, percent number, and percent volume were evaluated. Of the 1,041 stomachs that were examined for food, 436 were empty. The mean volume of food in all stomachs analyzed was 36.9 mL, of which 18.9 mL was bait and 18.0 mL was prey.

The gonostomatid *Maurolicus muelleri* and the euphausiid *Euphausia similis* were the principal foods. Other important foods were the chub mackerel, *Scomber japonicus*; the frigate tuna, *Auxis thazard*; gempylids; trichiurids; and carangids. In the study area, adult skipjack tuna were not found to feed on their young.

Kruskall-Wallis nonparametric one-way analysis of variance was used to test for differences in the mean volumetric ratios of food items in relation to skipjack size. The percentage of *E. similis* in the diet was found to decrease, while the proportion of *M. muelleri* was found to increase with increasing skipjack size. Seasonal variations in the diet were also examined and discussed.

Apparently the anatomy of their gill raker apparatus allows skipjack to ingest a wide variety of prey types above a minimum size. These variations in the food can be attributed to the number and size of the prey species in an area.

A Brazilian skipjack pole-and-line fishery has been developing in the Rio de Janeiro area since 1979 (Fig. 1). Because skipjack tuna, *Katsuwonus pelamis*, is one of the major tuna species harvested at maximum sustainable yield in the tropical and subtropical oceans (Kearny 1976; Evans et al. 1981), estimation of the fishery potential requires information on the distribution and concentration of its spawning stock. One technique used to determine the existence of a spawning stock is to quantify the distribution of its larvae. Obviously, the presence of large numbers of larvae would indicate a spawning stock occupies an area.

Knowledge of the distribution and abundance of juvenile skipjack tuna is limited. Occasionally, specimens have been found in experimental plankton hauls or in the stomachs of apex predators (Kearny 1976). From ichthyoplankton surveys, Matsuura (1982) and Nishikawa et al. (1978) reported larvae in warm tropical waters north of the study area (Fig. 1), and juvenile skipjack tuna have been found in the stomachs of adult skipjack tuna captured off west Africa and in the Caribbean (Suarez-Caabro and Duarte-Bello 1961; Klawe 1961; Dragovich 1970; Dragovich and Potthoff 1972). Their occurrence in the diet of central and south Pacific skipjack tuna caught by pole-and-line has been used to deduce their distribution and abundance (Waldron and King 1963; Nakamura 1965; Argue et al. 1983).

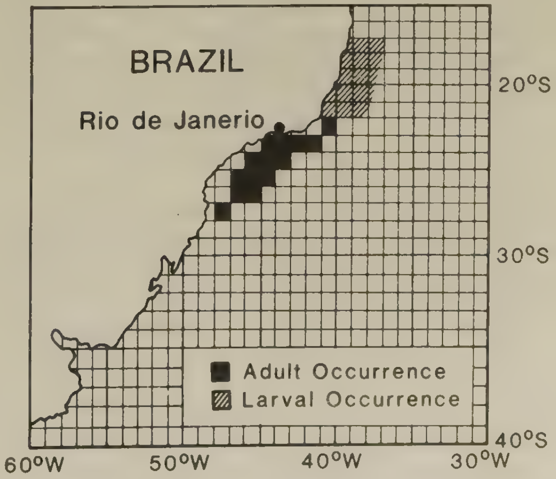

FIGURE 1.–Solid area indicates fishing localities from where skipjack tuna stomachs were obtained. Hatched area shows larval occurrence (Matsuura 1982).

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Dragovich (1969) reviewed existing information on the food habits of Atlantic skipjack tuna. Since that time food habits have also been reported in studies by Dragovich (1970) and Dragovich and Potthoff (1972) for skipjack from the East and West Atlantic and by Batts (1972) for skipjack in North Carolina waters. Zavala-Camin (1981) examined predator-prey interactions of fishes, including skipjack captured north of the area in this study.

The primary objective of this study was to discover if skipjack tuna feed upon their young. The presence of juveniles in bait-caught skipjack stomachs would verify the study area as a spawning-rearing ground. Knowledge of the prey and their relative importance also contributes to the understanding of prey-predator interactions, which affect population distributions and fluctuations.

MATERIALS AND METHODS

Stomach samples for this study were collected on a monthly basis from October 1981 to December 1982 from skipjack tuna caught off Rio de Janeiro (Fig. 1). National Marine Fisheries Service (NMFS) personnel collected stomachs from frozen fish transhipped to Puerto Rico, and Superintendencia do Desenvolviemento da Pesca (SUPEDE) personnel sampled fish landed locally in Rio de Janeiro. Fish from the Puerto Rican source were caught within 1 mo prior to sampling; fish from the Brazilian source were sampled 3 to 5 d after the recorded catch date. The sampling design required collecting about 15 stomachs from each 10 cm length group, measured to the nearest cm per month. However, the number of stomachs collected was dependent on the catch-size distribution. Once the stomach was removed from the fish, it was preserved in 10% buffered Formalin[2] and shipped to the Southwest Fisheries Center (SWFC) for analysis.

Stomachs were examined from 1,041 fish between 44 and 81 cm fork length. In the laboratory each stomach was opened. The volume of the food bolus was measured, and the contents were identified to the lowest possible taxon. The taxonomic groupings were then measured by volumetric displacement, and the individuals counted. Whole undigested fish were identified by comparing external characters with those described in published keys or with identified museum specimens from Scripps Institution of Oceanography, La Jolla, CA. Digested animals, particularly juvenile scombrids, were identified by vertebral, gill raker, and fin ray counts, as well as other skeletal characteristics, described by Potthoff and Richards (1970), Miller and Jorgenson (1973), and other published keys. Cephalopods were identified by comparing beak characters with published illustrations, descriptions, and keys (see Wolff 1981). Crustaceans and other invertebrates were identified by specialists from Scripps Institution of Oceanography and SWFC.

The occurrence of bait in the stomachs may have biased the relative importance of fish in the diet. The bait primarily consisted of *Sardinella brasiliensis*, *Harengula jaguana*, and *Engraulis anchoita*; however, other fish families may have been included in the captured bait. The sardines were readily identifiable from their external characters and usually were undigested. The anchovies, in contrast, were often quite digested, creating difficulties in identification. Gary Nelson[3] nevertheless was able to verify these fish as *Engraulis anchoita*. Although the least digested item in the stomach was usually the last meal (bait), stomachs were removed from a few days to 1 mo after capture, and presumably postmortem digestion occurred. As a result, the degree of digestion was not a reliable indication of distinguishing bait from natural prey. The time required for complete gastric evacuation of smelt fed to skipjack tuna is estimated to be 12 h (Magnuson 1969). Although the bait was captured in nets from bays and estuaries (Rinaldo[4]), Matsuura et al. (1978, 1981) have confirmed that a spawning stock of *E. anchoita* does exist in waters inhabited by skipjack tuna. It is unlikely that the sardines served as prey for skipjack. However, I could not distinguish between *E. anchoita* consumed as natural food and as bait. Therefore, although these species were considered bait, some may have been ingested as natural food. Bait was not considered prey, and stomachs containing only these species were treated as empty.

Two methods of analysis were employed to rank the food items in terms of availability and importance to the skipjack tuna:

1) An index of relative importance (IRI) was calculated for each prey type in terms of numbers, volumes, and frequencies (Pinkas et al. 1971):

$$IRI = (N + V)F$$

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] G. J. Nelson, Department of Ichthyology, American Museum of Natural History, New York, NY 10024, pers. commun., May 1982.

[4] R. R. Rinaldo, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun., June 1982.

where N = numerical percentage
V = volumetric percentage
F = frequency of occurrence percentage.

2) The mean volumetric ratio measurement (*MVRM*) was used to illustrate the biomass importance of prey items without the numeric exaggeration implicit in the *IRI* (John Hedgepeth[5]). The *MVRM* was calculated from the volumetric analysis of individual stomachs with each prey item contributing to the total stomach volume. *MVRM* for each food type is expressed as

$$MVRM = \bar{r}_j \times 100 = \text{mean volumetric percentage of prey } j \text{ to the total volume of } n \text{ stomachs}$$

where N = number of stomachs in a given strata
V_{ij} = volume of prey type j in stomach i

$$V_i = \sum_{j=1}^{6} V_{ij} = \text{total volume of stomach } i$$

$$r_{ij} = \frac{V_{ij}}{V_i} = \text{ratio of prey } j \text{ to the total volume of stomach } i$$

$$\bar{r}_j = \frac{\sum_{i=1}^{n} r_{ij}}{n} = \text{mean volumetric ratio of prey } j \text{ to the total volume of } n \text{ stomachs.}$$

Both the *IRI* and the *MVRM*, which examine different aspects of the diet, were used to evaluate seasonal variations in skipjack tuna food habits. The *IRI* presents a biased estimate caused by the numerical percentage; the relative importance of small numerous organisms, like euphausiids, is exaggerated in the *IRI* because of their high numbers, when actually they may represent the same food value as a few large fish. The *MVRM* is an expression of frequency of occurrence and volume without a numeric bias, but does not provide any information on prey abundance. The *IRI* contains information on the availability of the prey in the environment in terms of numbers, while the *MVRM* provides an indication of its energetic importance to the fish.

The *MVRM*s were stratified by fish length and annual quarter (Fig. 2), and tested with the Kruskal-Wallis nonparametric one-way analysis of variance to evaluate differences in diet with changes in size.

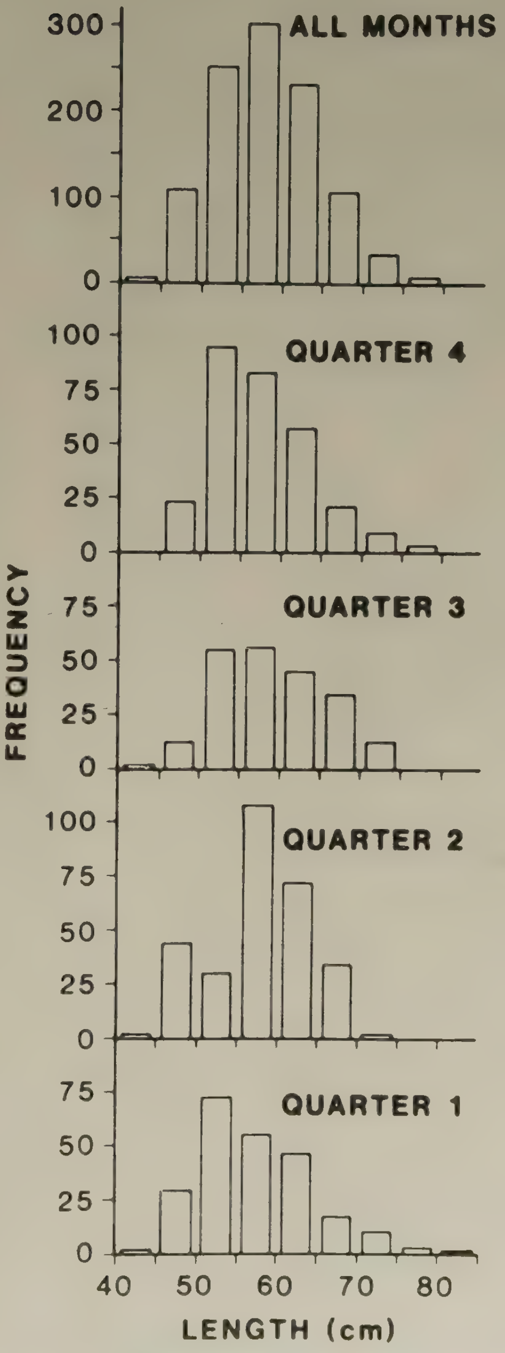

FIGURE 2.–Length-frequency distribution of skipjack tuna from which stomachs were collected.

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[5] J. B. Hedgepeth, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun., April 1982.

RESULTS

Food Composition

Of the 1,041 stomachs that were examined, 436 were empty. The mean volume of food in all stomachs examined was 36.9 mL, of which 18.9 mL was bait and 18.0 mL was prey. A complete list of the stomach contents in terms of numbers, volume, and frequency is presented in Appendix Table 1. No larval or juvenile skipjack were found in the stomach contents. Overall contributions of each category are presented in Figure 3.

In terms of the *MVRM*, the gonostomatid *Maurolicus muelleri* was the major prey item (*MVRM* = 26.7%). The euphausiid *Euphausia similis*, with the highest *IRI*, was also important (*IRI* = 1,998). These items were major constituents of the diet throughout the year. Other important fishes in terms of both the

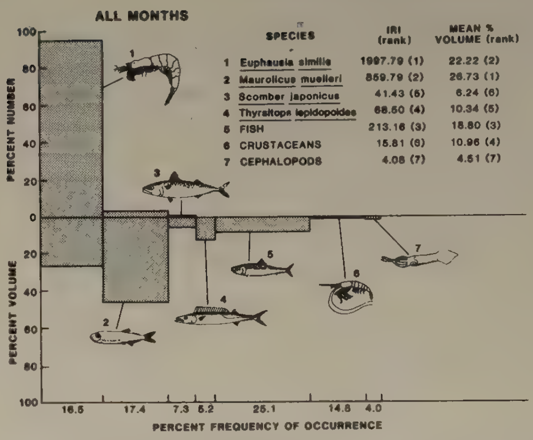

FIGURE 3.–Index of relative importance (IRI) plots for selected food items of skipjack tuna caught during 1982. The food categories are ranked in terms of IRI and MVRM.

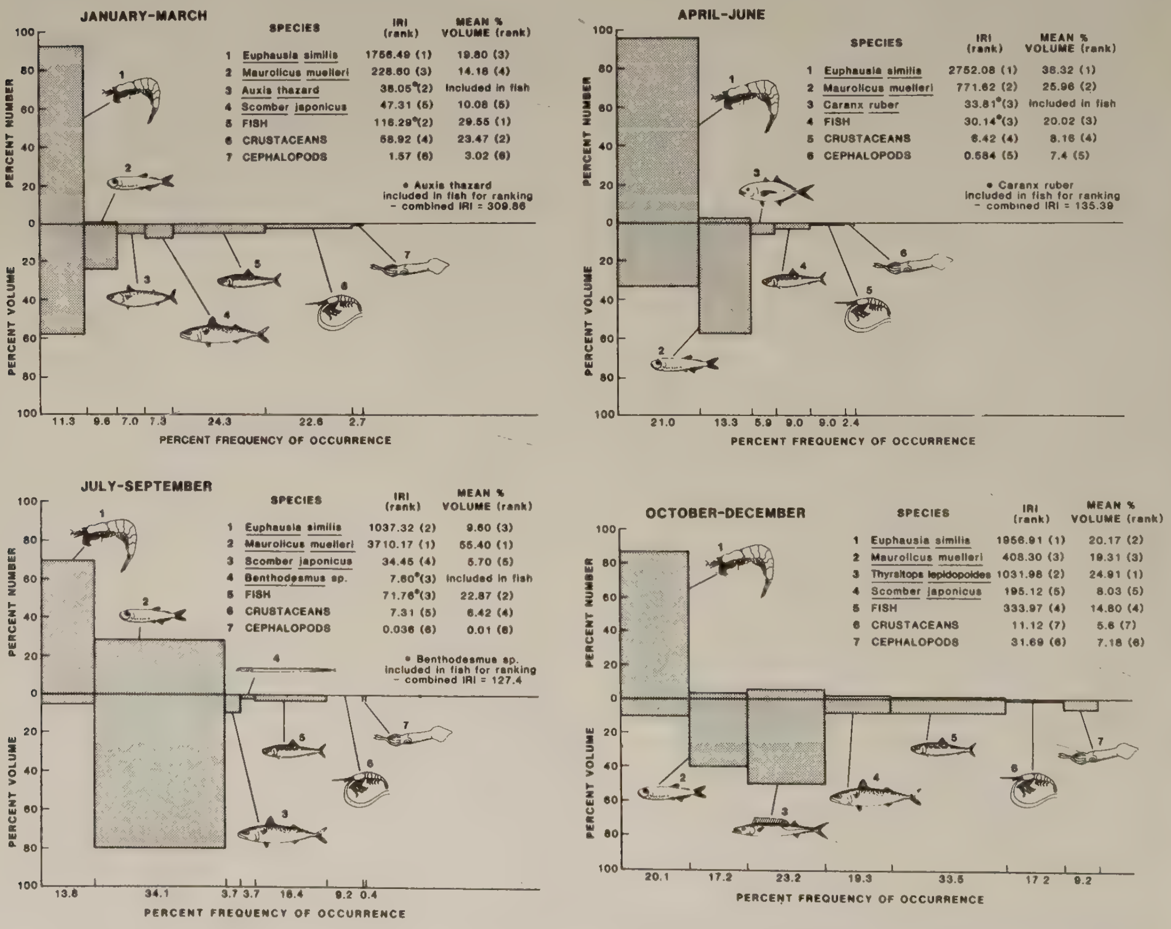

FIGURE 4.–Index of relative importance (IRI) plots for selected food items of skipjack tuna. The complete data are divided into four 3-mo quarters (I-IV). The food categories are ranked in terms of IRI and mean percent volume.

IRI and *MVRM* were chub mackerel, *Scomber japonicus*, and *Thyrsitops lepidopoides*[6] (Fig. 3). Crustaceans other than *E. similis* occurred frequently in the stomachs ($F = 22.6\%$), but as a relatively low percentage of the total volume ($V = 2.0\%$). Cephalopods were usually insignificant in the diet (see below). Pteropods, siphonophores, beetles, rocks, and unidentified materials were the constituents of the miscellaneous category (App. Table 1).

Seasonal Variations

The data were divided into four quarters: January-March 1982 (I), April-June 1982 (II), July-September 1982 (III), October-December 1981 and 1982 (IV). The results (App. Tables 2-6) are illustrated in Figures 4 and 5 both with the *IRI* and the *MVRM* of dominant food items in each quarter. Note that items important in one quarter may be negligible or absent in another. When evaluated in terms of *MVRM*, the prey ranks sometimes did not coincide with those determined by the *IRI* (Figs. 4, 5). Based on the *IRI*, *E. similis* was the dominant food in the first quarter, followed by other fish and *M. muelleri* (Fig. 4). According to the *MVRM*, other fishes, other crustaceans, and *E. similis* were ranked first, second, and third in importance, respectively. The importance of *E. similis* in this quarter based on the *IRI* was exaggerated by their high frequencies of occurrence. *Scomber japonicus* and frigate tuna, *Auxis thazard*, were secondary in importance to *M. muelleri* as the main fish species consumed.

The rankings of the food categories in the second quarter were the same for both the *IRI* and the *MVRM* (Fig. 4). *Euphausia similis* and *M. muelleri* were the dominant food items, followed by *Caranx ruber*.

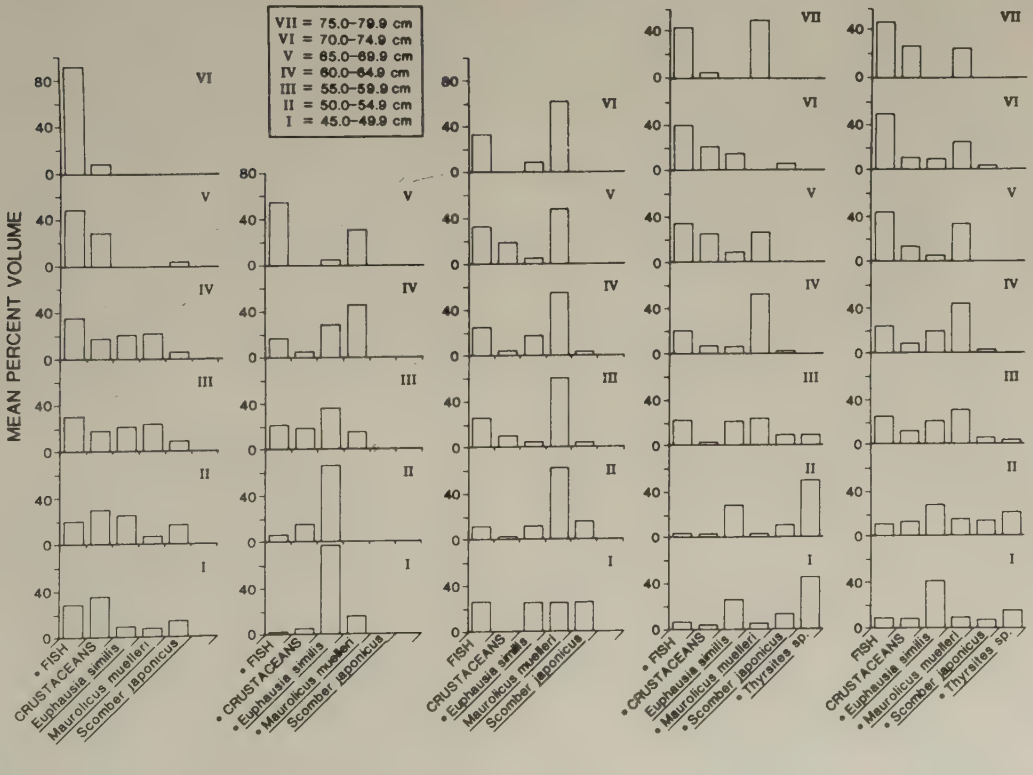

FIGURE 5. – Relative importance based on mean volumetric ratio of selected food items for skipjack tuna grouped by length for each quarter (I-IV) and all months. * indicates a significant difference ($P < 0.05$) in the mean percent volume of that food item by length when tested with the Kruskal-Wallis nonparametric one-way analysis of variance.

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[6] Identified by Y. Matsuura, Universidade de São Paulo, Instituto Oceanografico, São Paulo, Brazil, October 1984.

The principal food item in the third quarter based on both measurements was *M. muelleri* (Fig. 4). The ranks for the other items did not correspond. *Euphausia similis* was second in importance according to the *IRI*, but ranked third next to other fish based on the *MVRM*. *Scomber japonicus* and *Benthodesmus* sp. were the predominant species consumed in the fish category.

The *IRI* and *MVRM* ranks in the fourth quarter corresponded with the exception of the principal prey type (Fig. 4). Again, *E. similis* ranked first according to the *IRI*, but *Thyrsitops lepidopoides* was the primary food item based on the *MVRM*. Cephalopods, mainly *Argonauta* sp., were consumed in significant proportions in this quarter (*IRI* = 31.7, *MVRM* = 7.2%).

In summary, *M. muelleri* and *E. similis* predominated in the skipjack tuna diet during all quarters (Fig. 3). With the exception of the second quarter, *S. japonicus* was an important food item. *Benthodesmus* sp., *C. ruber*, *A. thazard*, as well as the cephalopod, *Argonauta* sp., also proved important in specific quarters. The importance of *T. lepidopoides* in Figure 3 was exaggerated by its predominance in the fourth quarter.

Variations with Size

As might be expected, basic dietary changes occur as the skipjack tuna grow. Nakamura (1965), Alverson (1963), Batts (1972), Dragovich and Potthoff (1972), and Wilson (1982) observed a decrease in the relative importance of crustaceans and an increasing importance of fish in the diet, as the skipjack size increased.

To evaluate the relationship between size and food habits, the skipjack were arbitrarily divided into seven 5 cm groups (Fig. 2). For each prey category the *MVRM*s were stratified by size group and quarter (App. Tables 6-10, Fig. 5). Trends reported in the results for length groups > 70 cm may not represent feeding habits of skipjack tuna from the study area because the sample sizes were too small (Fig. 2, App. Table 6).

There were no significant differences ($P < 0.05$) in diet and size in the first quarter except in the amount of other fish consumed (Fig. 5, App. Table 7). The *MVRM* of this category increased from 28.7% in skipjack 45.0-49.9 cm to 91.7% in fish 75.0-79.9 cm.

In the second quarter the proportions of other fish, other crustaceans, *E. similis*, and *M. muelleri* significantly changed with size (Fig. 5, App. Table 8). The larger skipjack tuna ate more fish (*MVRM* = 1.7% in the 45.0-49.9 cm size class to *MVRM* = 54.1% in the 75.0-79.9 cm size class) and more *M. muelleri* (*MVRM* = 15.4% to *MVRM* = 30.3%) than the smaller skipjack. As their size increased, skipjack decreased their consumption of *E. similis* from MVRM = 76.9% to *MVRM* = 4.5%. There was a significant difference between size classes ($P < 0.05$) in the *MVRM* of other crustaceans in the diet, but this difference seemed uncorrelated to increases in size.

In the third quarter there were no significant differences in the diet with increasing size except that the *MVRM* of *E. similis* decreased from 25.0% to 8.0% (Fig. 5, App. Table 9).

Thyrsitops lepidopoides was eaten by the smaller skipjack (45-59.9 cm) only in the fourth quarter (Fig. 5, App. Table 10). Although there were significant differences ($P < 0.05$) in the diets between the seven size groups during this period, these differences again seemed unrelated to increasing size.

In summary, when the data on *T. lepidopoides* were included with the rest of the fish data, there were no significant differences between size groups in the proportions of other fish consumed throughout the year (Fig. 5, App. Table 6). The *MVRM* of *E. similis* in the diet decreased from 42.5% in skipjack tuna 45.0-49.9 cm to 0.0% in skipjack 75.0-79.9 cm. There were significant differences in the percentages of *M. muelleri* and *S. japonicus* between the size classes. There were no significant differences in the *MVRM* of other crustaceans with changes in size.

As reported in the studies of the food habits of skipjack tuna referred to above, the stomach contents of skipjack from this area indicated the basic dietary changes associated with increasing size: a significant decrease in the proportion of *E. similis*, the predominant crustacean prey, and an increase in proportion of *M. muelleri*, the predominant fish prey.

DISCUSSION

Several studies have reported that skipjack tuna feed predominantly on euphausiids and gonostomatids. Dragovich and Potthoff (1972) reported that the gonostomatid *Vinciguerria nimbaria* contributed 44.7% by volume to the diet of skipjack tuna from the Gulf of Guinea. Zavala-Camin (1981) reported *M. muelleri* and euphausiids as dominant food items in 36 stomachs of skipjack caught off Brazil. Alverson (1963) reported skipjack tuna captured in the eastern tropical Pacific fed primarily on euphausiids (47% by volume, in 37% of the stomachs), followed in importance by the gonostomatid *Vinciguerria lucetia* (10% by volume). The abundance of euphausiids in the stomachs of skipjack, compared with larger scombrids, may be a result of smaller gill raker gaps in skipjack (Magnuson and Heitz 1971).

The importance of other fishes as food for western Atlantic skipjack tuna observed in this study has been previously reported. Dragovich (1970) found a predominance of fish in the stomachs of skipjack caught off the eastern United States and the Caribbean. Suarez-Caabro and Duarte-Bello (1961) found that fishes constituted 75% of the total volume, followed by squid (23%) and crustaceans (2%), in the stomachs of Cuban skipjack. Zavala-Camin (1981) observed that fish constituted 38.9%, crustaceans 22.2%, and mollusks 2.8% of the total stomach volume of Brazilian skipjack.

CONCLUSIONS

The multiplicity of prey found in this as well as other studies indicates that tunas are perhaps nonselective feeders, and stomach contents are probably determined by prey availability (Hotta and Ogawa 1955; Alverson 1963; Batts 1972; Perrin et al. 1973; Argue et al. 1983). Therefore, if the larval and juvenile skipjack were available in significant numbers, then one would expect them to occur in the diet of the adults.

Their absence in the diet was caused by two possible results. First, the young remained among the unidentified portion of the stomach contents; however, skipjack tuna have distinctive vertebral characteristics which were probably not discounted in the analysis (Potthoff and Richards 1970). Second, the adults did not spawn in the study area. Young skipjack should be found in the stomach contents of spawning adults (Argue et al. 1983). Goldberg and Au[7] found no evidence of spawning in skipjack collected from the Brazilian fishery. These results are consistent with the absence of larval and juvenile skipjack in the diet of the adults in this study.

The southernmost distribution boundary for larval skipjack tuna is the 24°C surface isotherm (Argue et al. 1983). Matsuura (1982) found no larval skipjack in ichthyoplankton surveys south of lat. 21°S in this area, where temperatures range from 21° to 24°C (Evans et al. 1981).

These results are consonant with those of Argue et al. (1983); juvenile skipjack tuna were absent from samples of adult stomachs taken in subtropical south Pacific waters. The adult skipjack in this investigation did not feed on their young. The absence of cannabilism suggests that larvae and juveniles were not significantly abundant to serve as forage of the adults, and therefore probably do not occur in this cooler southern water.

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LITERATURE CITED

ALVERSON, F. G.
1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 7:293-396.

ARGUE, A. W., F. CONAND, AND D. WHYMAN.
1983. Spatial and temporal distributions of juvenile tunas from stomachs of tunas caught by pole-and-line gear in the central and western Pacific Ocean. Tuna and Billfish Assessment Programme Technical Report No. 4. South Pacific Commission, Noumea, New Caledonia.

BATTS, B. S.
1972. Food habits of the skipjack tuna, *Katsuwonus pelamis*, in North Carolina waters. Chesapeake Sci. 13:193-200.

DRAGOVICH, A.
1969. Review of studies of tuna food in the Atlantic Ocean. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 593, 21 p.
1970. The food of skipjack and yellowfin tunas in the Atlantic Ocean. Fish. Bull., U.S. 68:445-460.

DRAGOVICH, A., AND T. POTTHOFF.
1972. Comparative study of food of skipjack and yellowfin tunas off the coast of West Africa. Fish. Bull., U.S. 70:1087-1110.

EVANS, R. H., D. R. MCLAIN, AND R. A. BAUER.
1981. Atlantic skipjack tuna: influences of mean environmental conditions on their vulnerability to surface fishing gear. Mar. Fish. Rev. 43(6):1-11.

HOTTS, H., AND T. OGAWA.
1955. On the stomach contents of the skipjack, *Katsuwonus pelamis*. Bull. Tohoku Reg. Fish. Res. Lab. 4:62-82.

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[7] Goldberg, S. R., and D. W. K. Au. 1983. The spawning schedule of skipjack tuna from southeastern Brazil as determined from histological examinations of ovaries, with notes on spawning in the Caribbean. Prepared for the International Skipjack Year Program conference of the International Commission for the Conservation of Atlantic Tunas, June 21-25, 1983, Tenerife, Canary Islands, Spain, 31 p. Manuscript in preparation; Department of Biology, Whittier College, Whittier, CA 90608.

KEARNEY, R. E.

1976. Some hypotheses on skipjack (*Katsuwonus pelamis*) in the Pacific Ocean. South Pac. Comm., Occas. Pap. 7, 23 p.

KLAWE, W. L.

1961. Young scombroids from the waters between Cape Hatteras and Bahama Islands. Bull. Mar. Sci. Gulf Caribb. 11: 150-157.

MAGNUSON, J. J.

1969. Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Trans. Am. Fish. Soc. 98:379-392.

MAGNUSON, J. J., AND J. G. HEITZ.

1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. Fish Bull., U.S. 361-370.

MATSUURA, Y.

1982. Distribution and abundance of skipjack (*Katsuwonus pelamis*) larvae in eastern Brazilian waters. ICCAT/SCRS/81/70, Coll. Vol. Sci. Pap. Vol. XVII (SCRS-1981), p. 211-213.

MATSUURA, Y., K. NAKATANI, G. SATO, AND S. T. J. TAMASSIA.

1978. Exploracão e avaliacão de estoque de peixes pelágicos no sul do Brasil. Relat. Técn. Conv. FINEP/IOUSP, 46 p.

MATSUURA, Y., J. C. AMARAL, S. T. J. TAMASSIA, AND G. SATO.

1981. Ocorrência de cardumes de peixes pelágicos e a estrutura oceanográfica da região entre Cabo de São Tomé (RJ) e Cananéla (SP) em janeiro-fevereiro de 1979. Sér. Doc. Técn. PDP/SUDEPE 36:1-73.

MILLER, G. L., AND S. C. JORGENSON.

1973. Meristic characters of some marine fishes of the western Atlantic Ocean. Fish Bull., U.S. 71:301-312.

NAKAMURA, E. L.

1965. Food and feeding habits of skipjack tuna (*Katsuwonus pelamis*) from the Marquesas and Tuamotu Islands. Trans. Am. Fish. Soc. 94:236-242.

NISHIKAWA, Y., S. KIKAWA, M. HONMA, AND S. UEYANAGI.

1978. Distribution atlas of larval tuna, billfishes, and related species. Results of larval surveys by R/V Shunyo-Maru and Shoyo-Maru, 1956-1975. Far Seas Fish. Res. Lab., S. Ser., 9:1-99.

PINKAS, L., M. S. OLIPHANT, AND L. K. IVERSON.

1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.

1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed species aggregations. Fish. Bull., U.S. 71:1077-1092.

POTTHOFF, T., AND W. J. RICHARDS.

1970. Juvenile bluefin tuna, *Thunnus thynnus* (Linnaeus), and other scombrids taken by terns in the Dry Tortugas, Florida. Bull. Mar. Sci. 20:389-413.

SUÁREZ-CAABRO, J. A., AND P. P. DUARTE-BELLO.

1961. Biologia pesquera del bonito (*Katsuwonus pelamis*) y la albacora (*Thunnus atlanticus*) en Cuba I. Inst. Cub. Invest. Tecnol. Ser. Estud. Trab. Invest. 15, 151 p.

WILSON, M. A.

1982. The reproductive and feeding behavior of skipjack tuna, *Katsuwonus pelamis*, in Papua New Guinea waters. D.P.I. Fish. Res. Surv. Br., Papua New Guinea, Rep. 82-4, 38 p.

WOLFF, G. A.

1981. A beak key for eight eastern tropical Pacific cephalopod species with relationships between their beak dimensions and size. Fish. Bull., U.S. 80:357-370.

ZAVALA-CAMIN, L. A.

1981. Habitos alimentares e distribuicao dos atuns e afins (Osteichthyes - Teleostei) e suas relacoes ecologicas com outras especies pelagicas das regioes Sudeste e Sul do Brasil. Ph.D. Thesis, Universidade de São Paulo, Sao Paulo, Brasil, 237 p.

1982. Datos historicos de areas de crecimiento de listado (*Katsuwonus pelamis*) obtenidos por medio de examen de contenido estomacal de predadores (informe preliminar). ICCAT/SCRS/82/48, Coll. Vol. Sci. Pap. Vol. XVII (SCRS-1981), p. 209-210.

APPENDIX

APPENDIX TABLE 1.—List of prey items and other ingested materials found in the stomachs of 1,041 skipjack tuna caught off southern Brazil, from October 1981 to December 1982.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	12.0	0.003	4.5	0.024	6.0	0.576
Mysidacea						
Eucopiidae	220.0	0.057	42.4	0.226	22.0	2.113
Lophogastridae	24.0	0.006	1.7	0.009	3.0	0.288
Isopoda	1.0	0.000	0.1	0.001	1.0	0.096
Flabellifera	7.0	0.002	2.1	0.011	7.0	0.672
Amphipoda	22.0	0.006	1.5	0.008	2.0	0.192
Gammaridea	16.0	0.004	5.1	0.027	10.0	0.961
Euphausiidae	139.0	0.036	3.9	0.021	15.0	1.441
Euphausia sp.	50.0	0.013	0.6	0.003	1.0	0.096
Euphausia similis	368,632.0	94.785	4,895.3	26.122	172.0	16.523
Stylocheiron sp.	1.0	0.000	0.3	0.002	1.0	0.096
Caridea	3.0	0.001	2.3	0.012	3.0	0.288
Macrura						
Scyllaridae	1.0	0.000	0.2	0.001	1.0	0.096
Unid. Phyllosoma larvae	1.0	0.000	0.1	0.001	1.0	0.096

APPENDIX TABLE 1.— *Continued.*

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Brachyura	5.0	0.001	0.7	0.004	1.0	0.096
Portunidae	1.0	0.000	0.1	0.001	1.0	0.096
Unid. megalops	102.0	0.026	32.0	0.171	27.0	2.594
Unid. zooea	555.0	0.143	30.2	0.161	24.0	2.305
Unid. Decapoda	7.0	0.002	0.6	0.003	2.0	0.192
Unid. Crustacea	96.0	0.025	11.0	0.059	26.0	2.498
Mollusca						
Gastropoda	1.0	0.000	0.1	0.001	1.0	0.096
Cavolina sp.	101.0	0.026	6.0	0.032	7.0	0.672
Cephalopoda						
Teuthoidea	4.0	0.001	26.0	0.139	4.0	0.384
Thysanoteuthidae	2.0	0.001	10.0	0.053	1.0	0.096
Ommastrephidae	35.0	0.009	55.1	0.294	18.0	1.729
Loliginidae	2.0	0.001	10.5	0.056	2.0	0.192
Histioteuthidae	1.0	0.000	1.0	0.005	1 0	0.096
Onychoteuthidae	13.0	0.003	6.0	0.032	2.0	0.192
Octopoda						
Argonautidae						
Argonauta sp.	20.0	0.005	75.9	0.405	11.0	1.057
Unid. Cephalopoda	4.0	0.001	1.3	0.007	3.0	0.288
Insecta						
Coleoptera	2.0	0.001	2.0	0.011	2.0	0.192
Siphonophora	1.0	0.000	0.9	0.005	1.0	0.096
Algalmidae	8.0	0.002	6.6	0.035	8.0	0.768
Pisces						
Gonostomatidae						
Maurolicus muelleri	13,438.0	3.455	8,619.3	45.994	181 0	17.387
Synodontidae	8.0	0.002	16.0	0.085	3.0	0.288
Paralepididae	1.0	0.000	0.5	0.003	1.0	0.096
Myctophidae	43.0	0.011	62.3	0.332	5.0	0.480
Exocoetidae	2.0	0.001	2.0	0.011	2.0	0.192
Exocoetus volitans	1.0	0.000	56.0	0.299	1.0	0.096
Scomberesocidae						
Scomberesox saurus	8.0	0.002	105.0	0.560	6.0	0.576
Belonidae	2.0	0.001	5.0	0.027	2.0	0.192
Macrorhamphosidae	5.0	0.001	6.9	0.037	4.0	0.384
Sygnathidae	1.0	0.000	1.0	0.005	1.0	0.096
Holocentridae	3.0	0.001	4.0	0.021	1.0	0.096
Holocentrus sp.	3.0	0.001	9.0	0.048	1.0	0.096
Carangidae	1.0	0 000	1.0	0.005	1.0	0.096
Selene vomer	8.0	0.002	17.0	0.091	8.0	0.768
Decapterus punctatus	2.0	0.001	46.0	0.245	2.0	0.192
Caranx ruber	70.0	0.018	360.0	1.921	17.0	1.633
Mullidae	11.0	0.003	25.0	0.133	6.0	0.576
Scombridae	16.0	0.004	2.5	0.013	3.0	0.288
Auxis thazard	474.0	0.122	223.7	1.194	23.0	2.209
Scomber japonicus	1,474.0	0.379	978.7	5.223	77.0	7.397
Sarda sarda	81.0	0.021	127.0	0.678	8.0	0.768
Gempylidae	176.0	0.045	100.7	0.537	20.0	1.921
Thyrsitops lepidopoides	2,617.0	0.673	2,348.4	12.532	54.0	5.187
Trichiuridae	11.0	0.003	12.0	0.064	4.0	0.384
Benthodesmus sp.	19.0	0.005	80.9	0.432	8.0	0.768
Unid. Perciforms	24.0	0 006	63.7	0.340	16.0	1.537
Balistidae	1.0	0.000	5.0	0.027	1.0	0.096
Monacanthidae	27.0	0.007	19.8	0.106	19.0	1.825
Ostraciidae	1.0	0.000	0.5	0.003	1.0	0.096
Molidae						
Ranzania sp.	3.0	0.001	13.0	0.069	1.0	0.096
Triglidae	1.0	0 000	1.0	0.005	1.0	0.096
Peristedion sp	1.0	0 000	1.0	0.005	1.0	0.096
Unid. fish	289.0	0.074	163.5	0.872	94.0	9.030
Unid. material	1.0	0 000	26.4	0.141	5.0	0.480
Empty					436.0	41.882
Total	388,912.0		18,739.9		1,041.0	

APPENDIX TABLE 2.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter I.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Mysidacea						
Eucopiidae	112.0	0.0076	9.3	0.253	8.0	2.658
Lophogastridae	19.0	0.013	1.5	0.041	2.0	0.664
Isopoda	1.0	0.001	0.1	0.003	1.0	0.332
Flabellifera	1.0	0.001	0.1	0.003	1.0	0.332
Amphipoda	20.0	0.014	0.5	0.014	1.0	0.332
Euphausiidae	49.0	0.033	2.3	0.063	4.0	1.329
Euphausia similis	144,070.0	97.624	2,125.9	57.878	34.0	11.296
Caridea	1.0	0.001	0.5	0.014	1.0	0.332
Brachyura						
Unid. megalops	80.0	0.054	22.6	0.615	17.0	5.648
Unid. zooea	549.0	0.372	28.6	0.779	19.0	6.312
Unid. Decapoda	4.0	0.003	0.1	0.003	1.0	0.332
Unid. Crustacea	47.0	0.032	8.3	0.226	13.0	4.319
Mollusca						
Gastropoda						
Pteropoda						
Cavolina	68.0	0.046	2.2	0.060	1.0	0.332
Cephalopoda						
Teuthoidea	2.0	0.001	2.0	0.054	2.0	0.664
Thysanoteuthidae	2.0	0.001	10.0	0.272	1.0	0.332
Ommastrephidae	5.0	0.003	1.1	0.030	2.0	0.664
Loliginidae	1.0	0.001	8.0	0.218	1.0	0.332
Octopoda						
Argonautidae						
Argonauta sp.	2.0	0.001	0.3	0.008	2.0	0.664
Insecta						
Coleoptera	1.0	0.001	1.0	0.027	1.0	0.332
Pisces						
Gonostomatidae						
Maurolicus muelleri	1,346.0	0.912	838.0	22.815	29.0	9.635
Belonidae	1.0	0.001	3.0	0.082	1.0	0.332
Holocentridae	3.0	0.002	4.0	0.109	1.0	0.332
Carangidae						
Selene vomer	6.0	0.004	9.0	0.245	6.0	1.993
Mullidae	2.0	0.001	8.0	0.218	1.0	0.332
Scombridae	15.0	0.010	1.5	0.041	2.0	0.664
Auxis thazard	427.0	0.289	189.7	5.165	21.0	6.977
Scomber japonicus	504.0	0.342	225.2	6.131	22.0	7.309
Gempylidae	76.0	0.051	48.5	1.320	11.0	3.654
Unid. Perciforms	9.0	0.006	7.0	0.191	5.0	1.661
Monacanthidae	13.0	0.009	9.5	0.259	8.0	2.658
Ostraciidae	1.0	0.001	0.5	0.014	1.0	0.332
Triglidae	1.0	0.001	1.0	0.027	1.0	0.332
Peristedion sp.	1.0	0.001	1.0	0.027	1.0	0.332
Unid. fish	137.0	0.093	76.5	2.083	35.0	11.628
Unid. material	1.0	0.001	26.3	0.716	4.0	1.329
Total	147,577.0		3,673.1		301.0	

APPENDIX TABLE 3.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter II.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	1.0	0.001	1.0	0.016	1.0	0.345
Mysidacea						
Eucopiidae	97.0	0.055	31.9	0.508	9.0	3.103
Lophogastridae	5.0	0.003	0.2	0.003	1.0	0.345
Isopoda						
Flabellifera	2.0	0.001	1.5	0.024	2.0	0.690
Amphipoda	2.0	0.001	1.0	0.016	1.0	0.345
Gammaridea	6.0	0.003	0.4	0.006	3.0	1.034
Euphausiidae	2.0	0.001	0.2	0.003	2.0	0.690
Euphausia similis	171,843.0	97.352	2,104.3	33.485	61.0	21.034
Caridea	1.0	0.001	0.8	0.013	1.0	0.345
Macrura						
Scyllaridae	1.0	0.001	0.2	0.003	1.0	0.345
Brachyura						
Unid. megalops	1.0	0.001	0.5	0.008	1.0	0.345
Unid. zooea	1.0	0.001	0.2	0.003	1.0	0.345
Unid. Decapoda	3.0	0.002	0.5	0.008	1.0	0.345
Unid. Crustacea	30.0	0.017	1.2	0.019	2.0	0.690
Mollusca						
Gastropoda						
Pteropoda						
Cavolina sp.	33.0	0.019	3.8	0.060	6.0	2.069
Cephalopoda						
Teuthoidea						
Ommastrephidae	6.0	0.003	8.5	0.135	5.0	1.724
Onychoteuthidae	13.0	0.007	6.0	0.095	2.0	0.690
Siphonophora						
Algalmidae	8.0	0.005	6.6	0.105	8.0	2.759
Pisces						
Gonostomatidae						
Maurolicus muelleri	4,287.0	2.429	3,548.0	56.458	38.0	13.103
Synodontidae	8.0	0.005	16.0	0.255	3.0	1.034
Myctophidae	24.0	0.014	61.3	0.975	4.0	1.379
Sygnathidae	1.0	0.001	1.0	0.016	1.0	0.345
Carangidae						
Selene vomer	2.0	0.001	8.0	0.127	2.0	0.690
Decapterus punctatus	2.0	0.001	46.0	0.732	2.0	0.690
Caranx ruber	70.0	0.040	360.0	5.729	17.0	5.862
Scombridae						
Auxis thazard	46.0	0.026	30.0	0.477	1.0	0.345
Scomber japonicus	8.0	0.005	6.0	0.095	2.0	0.690
Unid. Perciforms	1.0	0.001	12.0	0.191	1.0	0.345
Balistidae	1.0	0.001	5.0	0.080	1.0	0.345
Monacanthidae	4.0	0.002	4.1	0.065	3.0	1.034
Unid. fish	9.0	0.005	18.1	0.288	6.0	2.069
Total	176,518.0		6,284.3		290.0	

APPENDIX TABLE 4.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter III.

	Numbers		Volume		Occurrence	
Prey items	No.	%	mL	%	No.	%
Crustacea						
Mysidacea						
Eucopiidae	10.0	0.046	0.8	0.020	4.0	1.843
Isopoda						
Flabellifera	2.0	0.009	0.3	0.007	2.0	0.922
Euphausiidae	88.0	0.401	1.4	0.034	9.0	4.147
Euphausia sp.	50.0	0.228	0.6	0.015	1.0	0.461
Euphausia similis	15,414.0	70.236	196.3	4.796	30.0	13.825
Unid. Crustacea	5.0	0.023	0.4	0.010	4.0	1.843
Mollusca						
Cephalopoda						
Teuthoidea	1.0	0.005	3.0	0.073	1.0	0.461
Pisces						
Gonostomatidae						
Maurolicus muelleri	6,239.0	28.429	3,289.2	80.369	74.0	34.101
Exocoetidae	2.0	0.009	2.0	0.049	2.0	0.922
Exocoetus volitans	1.0	0.005	56.0	1.368	1.0	0.461
Macrorhamphosidae	2.0	0.009	2.9	0.071	2.0	0.922
Carangidae	1.0	0.005	1.0	0.024	1.0	0.461
Mullidae	6.0	0.027	9.0	0.220	3.0	1.382
Scombridae						
Scomber japonicus	45.0	0.205	374.0	9.138	8.0	3.687
Sarda sarda	6.0	0.027	4.0	0.098	2.0	0.922
Trichiuridae	11.0	0.050	12.0	0.293	4.0	1.843
Benthodesmus sp.	19.0	0.087	80.9	1.977	8.0	3.687
Unid. Perciforms	4.0	0.018	35.0	0.855	3.0	1.382
Monacanthidae	1.0	0.005	1.0	0.024	1.0	0.461
Unid. fish	39.0	0.178	22.8	0.557	21.0	9.677
Total	21,946.0		4,092.6		217.0	

APPENDIX TABLE 5.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter IV.

	Numbers		Volume		Occurrence	
Prey items	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	11.0	0.026	3.5	0.075	5.0	2.146
Mysidacea						
Eucopiidae	1.0	0.002	0.4	0.009	1.0	0.429
Isopoda						
Flabellifera	2.0	0.005	0.2	0.004	2.0	0.858
Amphipoda						
Gammaridea	10.0	0.023	4.7	0.100	7.0	3.004
Euphausiidae						
Euphausia similis	37,305.0	87.017	468.8	9.996	47.0	20.172
Stylocheiron sp.	1.0	0.002	0.3	0.006	1.0	0.429
Caridea	1.0	0.002	1.0	0.021	1.0	0.429
Macrura						
Scyllaridae						
Unid. Phyllosoma larvae	1.0	0.002	0.1	0.002	1.0	0.429
Brachyura	5.0	0.012	0.7	0.015	1.0	0.429
Portunidae	1.0	0.002	0.1	0.002	1.0	0.429
Unid. megalops	21.0	0.049	8.9	0.190	9.0	3.863
Unid. zooea	5.0	0.012	1.4	0.030	4.0	1.717
Unid. Crustacea	14.0	0.033	1.1	0.023	7.0	3.004
Mollusca						
Gastropoda						
Pteropoda						
Cavoliniidae	1.0	0.002	0.1	0.002	1.0	0.429
Cephalopoda						
Teuthoidea	1.0	0.002	21.0	0.448	1.0	0.429
Ommastrephidae	24.0	0.056	45.5	0.970	11.0	4.721
Loliginidae	1.0	0.002	2.5	0.053	1.0	0.429
Histioteuthidae	1.0	0.002	1.0	0.021	1.0	0.429
Octopoda						
Argonautidae						
Argonauta sp.	18.0	0.042	75.6	1.612	9.0	3.863
Unid. Cephalopoda	4.0	0.009	1.3	0.028	3.0	1.288
Insecta						
Coleoptera	1.0	0.002	1.0	0.021	1.0	0.429
Siphonophora	1.0	0.002	0.9	0.019	1.0	0.429
Pisces						
Gonostomatidae						
Maurolicus muelleri	1,566.0	3.653	944.1	20.130	40.0	17.167
Paralepididae	1.0	0.002	0.5	0.011	1.0	0.429
Myctophidae	19.0	0.044	1.0	0.021	1.0	0.429
Scomberesocidae						
Scomberesox saurus	8.0	0.019	105.0	2.239	6.0	2.575
Belonidae	1.0	0.002	2.0	0.043	1.0	0.429
Macrorhamphosidae	3.0	0.007	4.0	0.085	2.0	0.858
Holocentridae						
Holocentrus sp.	3.0	0.007	9.0	0.192	1.0	0.429
Mullidae	3.0	0.007	8.0	0.171	2.0	0.858
Scombridae	1.0	0.002	1.0	0.021	1.0	0.429
Auxis thazard	1.0	0.002	4.0	0.085	1.0	0.429
Scomber japonicus	917.0	2.139	373.5	7.964	45.0	19.313
Sarda sarda	75.0	0.175	123.0	2.623	6.0	2.575
Gempylidae	100.0	0.233	52.2	1.113	9.0	3.863
Thyrsitops lepidopoides	2,617.0	6.104	2,348.4	50.074	54.0	23.176
Unid. Perciforms	10.0	0.023	9.7	0.207	7.0	3.004
Monacanthidae	9.0	0.021	5.2	0.111	7.0	3.004
Molidae	1.0	0.001	0.5	0.014	1.0	0.332
Ranzania sp.	3.0	0.007	13.0	0.277	1.0	0.429
Unid. fish	104.0	0.243	46.1	0.983	32.0	13.734
Unid. material	0.0	0.000	0.1	0.002	1.0	0.429
Total	42,871.0		4,689.9		233.0	

APPENDIX TABLE 6.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for all months. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*	*Thyrsitops lepidopoides*
45.0-49.9(67)	9.51 ± 22.5	9.51 ± 25.4	42.50 ± 48.1	10.35 ± 29.5	8.57 ± 23.6	16.64 ± 36.4
50.0-54.9(155)	10.53 ± 27.7	12.62 ± 30.9	26.73 ± 43.6	13.99 ± 33.4	12.44 ± 29.5	20.05 ± 38.5
55.0-59.9(162)	24.81 ± 39.4	11.80 ± 29.5	20.40 ± 39.5	29.49 ± 43.6	5.62 ± 19.6	2.70 ± 14.2
60.0-64.9(147)	23.48 ± 39.2	8.03 ± 24.7	18.83 ± 36.5	42.90 ± 48.2	2.12 ± 12.2	—
65.0-69.9(55)	42.80 ± 47.6	12.43 ± 31.7	4.73 ± 18.7	32.18 ± 45.9	0.27 ± 2.0	—
70.0-74.9(13)	48.30 ± 48.1	9.88 ± 27.9	8.57 ± 21.9	23.36 ± 43.7	2.20 ± 79.2	—
75.0-79.9(4)	47.50 ± 55.0	27.50 ± 48.6	—	25.00 ± 50.0	—	—
Total (603)	18.80 ± 35.5	10.96 ± 28.6	22.22 ± 40.0	26.73 ± 42.8	6.24 ± 21.1	10.34 ± 27.9

APPENDIX TABLE 7.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter I. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(12)	28.70 ± 33.4	35.15 ± 42.5	9.18 ± 28.7	7.48 ± 25.9	13.89 ± 38.4
50.0-54.9(53)	19.87 ± 36.8	29.64 ± 43.5	24.48 ± 43.3	6.09 ± 19.6	16.12 ± 33.5
55.0-59.9(45)	30.23 ± 40.9	17.69 ± 33.9	20.81 ± 38.9	22.96 ± 38.1	7.98 ± 25.2
60.0-64.9(36)	34.79 ± 44.1	16.96 ± 35.4	20.14 ± 38.9	20.92 ± 40.1	19.84 ± 46.5
65.0-69.9(4)	48.61 ± 56.2	28.24 ± 47.9	—	—	3.71 ± 7.4
70.0-74.9(3)	91.67 ± 14.4	8.33 ± 14.4	—	—	—
75.0-79.9(2)	—	—	—	—	—
Total (155)	29.55 ± 41.0	23.47 ± 38.9	19.80 ± 38.9	14.18 ± 32.1	10.08 ± 27.3

APPENDIX TABLE 8.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter II. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(26)	1.65 ± 8.4	5.00 ± 20.3	76.92 ± 43.0	15.38 ± 36.8	—
50.0-54.9(12)	5.82 ± 11.5	14.72 ± 33.0	65.71 ± 48.6	—	—
55.0-59.9(35)	20.89 ± 38.7	18.13 ± 36.4	35.65 ± 49.9	14.71 ± 33.9	0.14 ± 0.80
60.0-64.9(45)	16.33 ± 36.2	4.67 ± 18.5	28.92 ± 45.7	45.54 ± 49.7	0.32 ± 2.1
65.0-69.9(23)	54.07 ± 49.1	—	4.49 ± 20.8	30.29 ± 46.8	—
Total (141)	20.02 ± 38.1	8.16 ± 25.2	38.32 ± 48.6	25.96 ± 43.3	0.14 ± 1.3

APPENDIX TABLE 9.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter III. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(4)	25.81 ± 49.5	—	25.00 ± 50.0	24.19 ± 48.4	25.00 ± 50.0
50.0-54.9(27)	11.17 ± 32.0	1.24 ± 6.4	11.21 ± 32.0	61.56 ± 48.5	14.81 ± 36.2
55.0-59.9(36)	24.88 ± 41.3	9.22 ± 27.9	3.67 ± 16.2	59.05 ± 47.0	3.17 ± 16.8
60.0-64.9(31)	24.09 ± 40.5	3.39 ± 17.9	16.51 ± 29.9	53.76 ± 46.6	2.26 ± 12.6
65.0-69.9(17)	31.80 ± 46.4	17.65 ± 39.3	3.89 ± 9.8	46.67 ± 48.8	—
70.0-74.9(5)	31.27 ± 45.5	—	8.00 ± 17.9	60.73 ± 53.8	—
Total (120)	22.87 ± 40.1	6.42 ± 23.6	9.6 ± 25.5	55.40 ± 47.39	5.70 ± 22.7

APPENDIX TABLE 10.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter IV. Data are $\bar{r}$ ± SD with (n) in parentheses. Range is 0-100%.

Length cm (n)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*	*Thyrsitops lepidopoides*
45.0-49.9(25)	5.86 ± 13.8	3.43 ± 11.0	25.49 ± 39.6	4.26 ± 16.9	12.30 ± 25.1	44.60 ± 48.4
50.0-54.9(63)	3.30 ± 13.4	2.77 ± 13.0	27.84 ± 43.4	2.91 ± 16.3	10.69 ± 25.1	49.33 ± 47.0
55.0-59.9(46)	22.45 ± 37.5	3.25 ± 15.3	21.48 ± 40.2	24.01 ± 42.9	9.40 ± 22.5	9.49 ± 25.7
60.0-64.9(35)	20.51 ± 35.4	7.29 ± 22.1	6.55 ± 19.5	52.48 ± 49.9	1.71 ± 85.6	—
65.0-69.9(11)	34.11 ± 44.1	24.59 ± 40.2	8.26 ± 27.4	25.45 ± 43.9	—	—
70.0-74.9(5)	39.31 ± 53.8	20.69 ± 44.4	14.29 ± 31.9	—	5.71 ± 12.8	—
75.0-79.9(2)	45.00 ± 63.6	5.00 ± 7.1	—	50.0 ± 70.7	—	—
Total (187)	14.80 ± 16.5	5.6 ± 19.5	29.17 ± 37.8	19.31 ± 38.9	8.03 ± 21.2	24.91 ± 27.7

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DOLPHIN HABITATS IN THE EASTERN TROPICAL PACIFIC

David W. K. Au and Wayne L. Perryman[1]

ABSTRACT

Research-ship surveys by the Southwest Fisheries Center provided information on the distributions of spotted, spinner, striped, and common dolphins in the eastern tropical Pacific. The main surveys were conducted from January to March during 1976, 1977, 1979, and 1980. Two ships were used per survey, and together they overlapped most areas in the eastern Pacific where dolphins and yellowfin tuna are jointly fished by purse seiners.

The spatial distribution of sightings and of sighting rate of these species show a complementarity to their patterns, although there is a broad overlap. Spotted and spinner dolphins occurred primarily in tropical waters north of the Equator, but also in the seasonal tropical waters south of the Galapagos Islands. These dolphins were relatively infrequent along the Equator, off Costa Rica, and northern South America. Common and striped dolphins tended to be more frequent in these same areas of less frequent spotted and spinner dolphins.

The differences in habitats of these two species pairs can be described in oceanographic terms. Spotted and spinner dolphins are primarily in Tropical Surface Water, centered off southern Mexico and extending westward along lat. 10°N, where thermocline "ridging" and relatively small annual variations in surface temperature are features. Common and striped dolphins appear to perfer equatorial and subtropical waters with relatively large seasonal changes in surface temperature and thermocline depth and with seasonal upwelling.

The species composition of various areas in the eastern tropical Pacific supports the contention of two major communities. South of where spotted and spinner dolphin schools predominate (along with Risso's, bottlenose, and rough-toothed dolphins), striped and common dolphins and also pilot whales become increasingly important. Observations along the Equator also suggest a fauna different from that of the Tropical Surface Water that is most characterized by spotted and spinner dolphins.

A trophic basis to these faunal differences is suggested by the interactions with fish and birds. Assuming the birds indicate co-occurring tuna, only the spotted and spinner dolphins are commonly found with fish. The distribution of these dolphins as they co-occur with bird flocks and tuna indicates that this interspecific association is confined primarily to the Tropical Surface Water and is a characteristic feature of its epipelagic community.

he eastern tropical Pacific Ocean supports producive tuna fisheries as well as an abundant and diverse etacean fauna. Tuna fishermen there take advanage of the fact that tuna and dolphins frequently swim together. In the "porpoise-tuna" fishery for yellowfin tuna, *Thunnus albacares*, spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris*, are temporarily caught by purse seiners in order to take the associated tuna. Striped and common dolphins, *S. coeruleoalba* and *Delphinus delphis*, are caught to a lesser extent for the same reason. These dolphins suffer incidental mortality in the fishery and, because of the resulting concern, the Southwest Fisheries Center has been studying their populations to better advise on their management (Smith 1983). Learning about their habitats is one aspect of these studies.

Perrin (1975a), using the information collected mainly aboard tuna seiners, first showed that the geographic distributions of spotted, spinner, and striped dolphins in the eastern Pacific are extensive, stretching westward from the American coasts past long. 145°W at about lat. 10°N and also dipping south and southwest of the Galapagos Islands. Evans (1975) showed that the common dolphin occurs offshore of Central America to about long. 112°W and also along the Equator, westward past the Galapagos Islands. Recent summaries of available information (Au et al. 1979[2]; Scott 1981; Perrin et al. 1983) have shown that the distributions of these dolphins are even more extensive than originally perceived. Indeed the species have been reported from localities across the entire Pacific (Alverson 1981).

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[2] Au, D. W. K., W. L. Perryman, and W. F. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Admin. Rep. LJ-79-43, 59 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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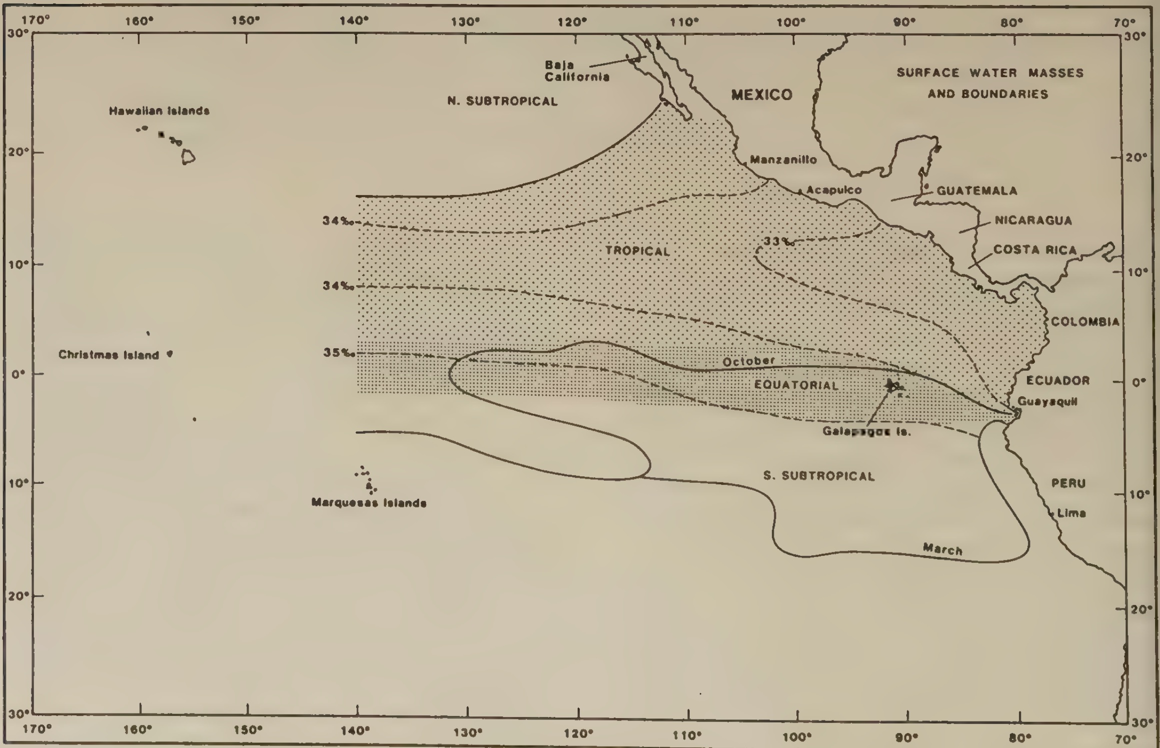
The purpose of this paper is to describe the January-March distributions of schools of spotted, spinner, striped, and common dolphins as determined from research ship surveys. Being independent and distinct from data collected by observers aboard tuna seiners, these survey data enable a separate evaluation of habitats and ecological relationships. The distributions derived will be discussed in terms of habitat features and interspecific associations including those of other cetaceans, yellowfin tuna, and certain seabirds. We propose that two major cetacean communities can be recognized, centered broadly about the tropical and about the equatorial-subtropical surface water provinces (Fig. 1).

METHODS

The Southwest Fisheries Center conducted or participated in 17 research cruises studying cetaceans between 1976 and 1981. Eight major cruises were carried out between January and March of 1976, 1977, 1979, and 1980, with the NOAA ships *David Starr Jordan* and *Townsend Cromwell*. During these surveys, schools of all cetacean species encountered (at least 23 species in the areas of interest) were approached to allow close observation. The combined cruise tracks of these January-March surveys formed an extensive coverage of the eastern tropical Pacific and included areas not frequently searched by fishing vessels (Fig. 2). The latter are the equatorial waters and areas both south of lat. 8°N and west of long. 110°W. The cruise tracks during any particular year were chosen to investigate certain aspects of dolphin distribution, e.g., the intensive surveys during 1979 off southern Mexico and central America constituted a joint aircraft-ship survey of the nearshore habitat. The remaining other nine cruises were either for special studies or of ships of opportunity. In the latter case, the ships did not usually divert course to inspect cetacean schools that were sighted.

Cetacean observations from a research ship were conducted by scanning the waters ahead and to the sides of the ship through 20 × 120 mm USN MK-3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Marquesas Islands
March

FIGURE 1.—Surface water masses and boundaries of the tropical ocean in the eastern Pacific, based on Wyrtki's (1964a, 1967) analysis to long. 140°W. Boundaries are a function of the 24°C surface isotherm and the 1°C/10 m thermocline gradient. Notice that in October the southern boundary to the eastern tropical ocean lies mostly north of the Equator, while in March this boundary lies far to the south so that southern subtropical waters become tropical.

or 25 × 150 mm Fuji binoculars, mounted both port and starboard either on or above the flying bridge. The sighting distance to the horizon was about 7.0 and 5.5 nmi for the *David Starr Jordan* and *Townsend Cromwell* respectively. Both ships cruised at about 10 kn (18.5 km/h). The cetacean search-day generally started at 0600 and ended 1800, with two teams, or watches, alternating. In 1976 and 1977 the watches were each 2 or 3 h long, depending on the ship. In 1979 and 1980 they were all standardized to 3 h. There were two experienced persons on each watch, who alternated each hour between the port and starboard binoculars. A third person sometimes helped in record keeping, obtaining supplementary data, and temporarily relieving the other watch members. The peripheral data collected included bathythermograms, surface temperature and salinity, weather observations, sighting condition measurements, sighting effort, and observations on fish and birds.

When a cetacean school was sighted, its angle relative to the ship's heading was measured and its distance from the ship estimated. The ship then approached the school for closer observation. School size was estimated and the species identified.

The reader is cautioned that the distributions to be described are based upon relatively few sightings of schools (Table 1) and that they pertain to the January-March season specifically. Though the pattern of sampling was widespread, the actual area surveyed was a very small fraction of the huge area

TABLE 1.—Summary of school sizes for spotted, spinner, striped, and common dolphins from the January-March research cruises of 1976, 1977, 1979, and 1980.

		Arithmetic		Geometric	
Species	n	$\bar{x}$	s	$\bar{x}$	s^1
Spotted[2]	157	148.52	300.93	65.55	3.56
Spotted and spinner	79	357.42	444.50	211.67	2.93
Spinner[3]	44	228.39	291.54	107.05	3.88
Striped	187	60.84	69.78	40.74	2.56
Common	98	261.16	484.64	108.47	3.72
Total[4]	565				

[1] Standard deviation factor for the geometric mean.

[2] Total spotted dolphin schools is 157 + 79 = 236.

[3] Total spinner dolphin schools is 44 + 79 = 123.

[4] Additionally, there were 838 school sightings of unidentified and other species of dolphins (Delphinidae) and 543 school sightings of whales (Balaenopteridae, Ziphiidae, and Physeteridae).

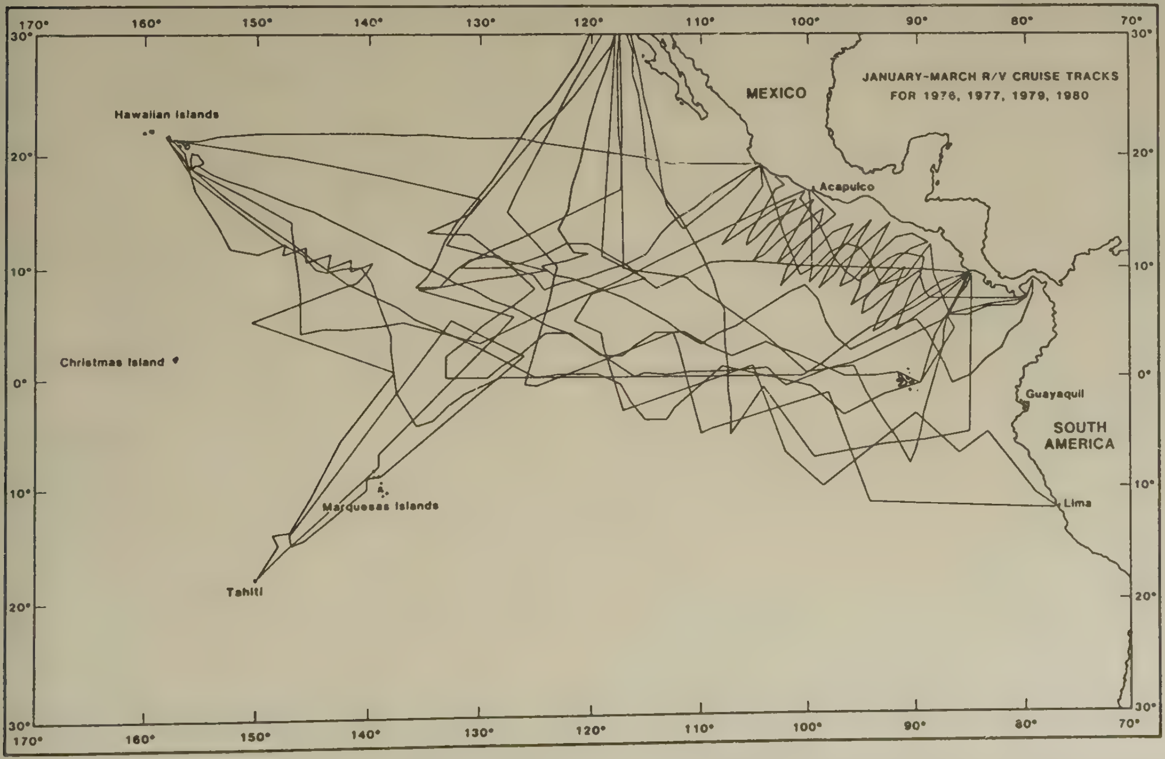

FIGURE 2.—Cruise tracks of the January-March cruises by RV *David Starr Jordan* and RV *Townsend Cromwell*. These cruises took place in 1976, 1977, 1979, and 1980.

of the eastern Pacific. The patterns of species distribution we describe will not always be obvious. Nevertheless there is evidence from other distribution studies, using data collected from the fishery, that these patterns are real (Perrin et al. 1983).

The results described in this paper are based upon our personal experiences at sea where the procedure of investigating all cetacean schools and continuously monitoring the physical and biotic environment enabled the development of an ecological understanding of these dolphins. Continuity in these studies was provided by the fact that on each ship there was at least one experienced observer who participated during all cruise years. We present our results as an independent, research-ship based, assessment of species distributions and habitat areas.

RESULTS

Distribution and Relative Abundance of Dolphin Schools

Plots of the sighting localities of schools of spotted, spinner, striped, and common dolphins, obtained during the January-March research cruises, show the geographical distributions of these species during the northern winter season. Table 1 summarizes the numbers and sizes of the schools which were identified and studied. Geographic locations referred to in the text can be found in Figure 1.

Spotted and spinner dolphins are often in mixed schools (33.5% of spotted dolphins schools also contained spinner dolphins, Table 1), and so the sightings of spotted or of mixed spotted plus spinner dolphin schools are shown together (Fig. 3). Most of the mixed schools were encountered off southern Mexico, where the eastern form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) usually accompanied spotted dolphins (cf. Figs. 3, 4). Mixed schools were uncommon along the Equator, as was the spotted dolphin itself, especially west of long. 110°W. Large schools (>300 individuals) of spotted dolphin were widely scattered, but tended to be more common off southern Mexico. Westward extensions of distribution appeared to occur as three main lobes: about lat. 10°n, between lat. 0° and 5°N, and between lat. 2°S and 5°S.

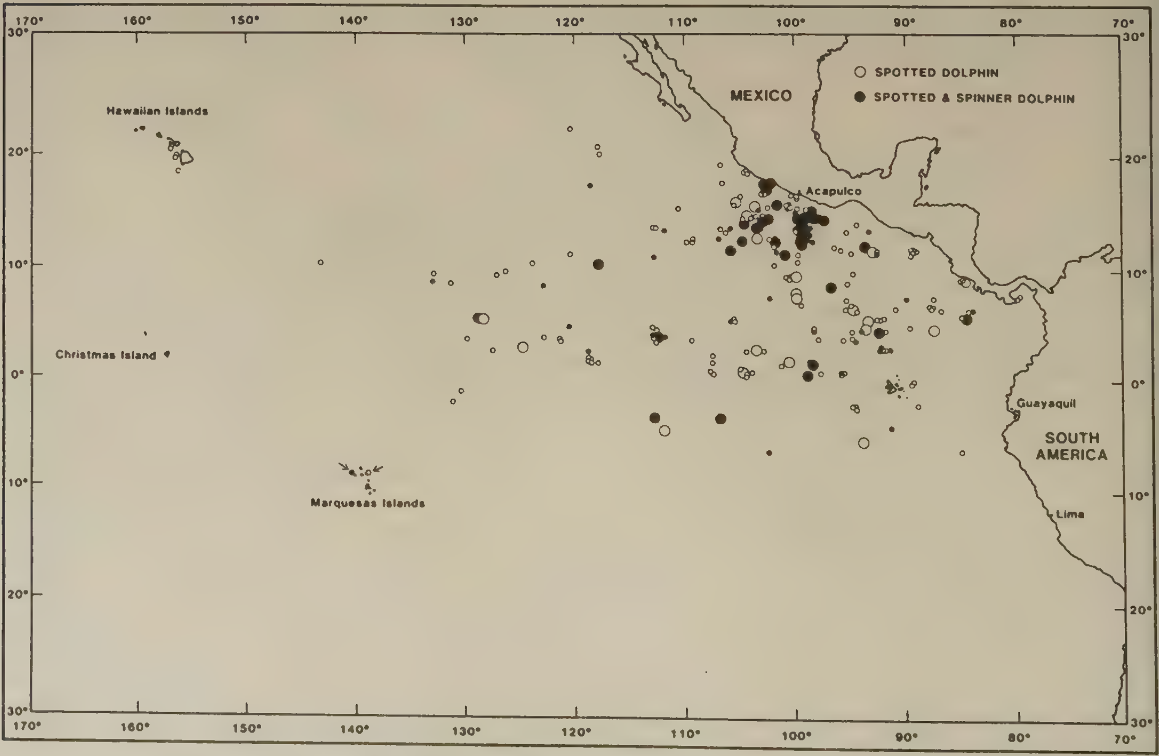

FIGURE 3.—Distribution of spotted and spotted plus spinner dolphin schools seen during the January-March research cruises. Larger circles indicate schools of >300 animals.

The spinner dolphin appears to be distributed like the spotted dolphin, with westerly extending lobes of distribution in similar latitudes (Fig. 4). Schools were infrequent along the Equator, more so than were those of spotted dolphin. The eastern spinner was encountered frequently off southern Mexico, where its main population center appeared to be relatively localized. However, eastern spinner dolphins were seen as far offshore as long. 126°W near lat. 10°N and also nearly to the Equator within a broad, 600 nmi coastal belt off Central America. The whitebelly form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) occurred in a broad range north and south of the Equator and at the southern and western portions of the total spinner dolphin range. Large schools (>300) were seen mostly off southern Mexico (eastern spinner) and south of the Equator (whitebelly spinner).

Striped and common dolphins seem to have a distribution pattern qualitatively different from that of spotted and spinner dolphins (Fig. 5). A distinct distributional lobe, consisting primarily of common dolphins, occurred off Baja California, with extensions around the Revilla Gigedo Islands (ca. lat. 19°N, long. 111°W). Between lat. 5° and 12°N, off Central America, there was a second lobe made up of both species. This lobe attenuated to the west along lat. 10°N, but appeared to re-intensify past long. 130°W. Only striped dolphins were seen in the intermediate interval between long. 100°W and 130°W along this lobe. A third lobe appeared to originate off Peru. It merged somewhat with the outer portions of the Central American lobe, and then extended westward along the Equator. Equatorial waters were frequented by both species out to about long. 100°W, beyond which striped dolphins apparently predominate. The striped dolphin is the more widespread of the two species; however, its school sizes are small (Table 1). Large schools (>300) of the common dolphin occurred within each of the three main centers of its distribution.

The above sighting data were adjusted to show the distributions of relative abundance of schools by correcting for searching effort. Effort is calculated as miles searched = time searched × ship speed. Relative abundance of schools was expressed as schools per 100 nmi searched (approximately the

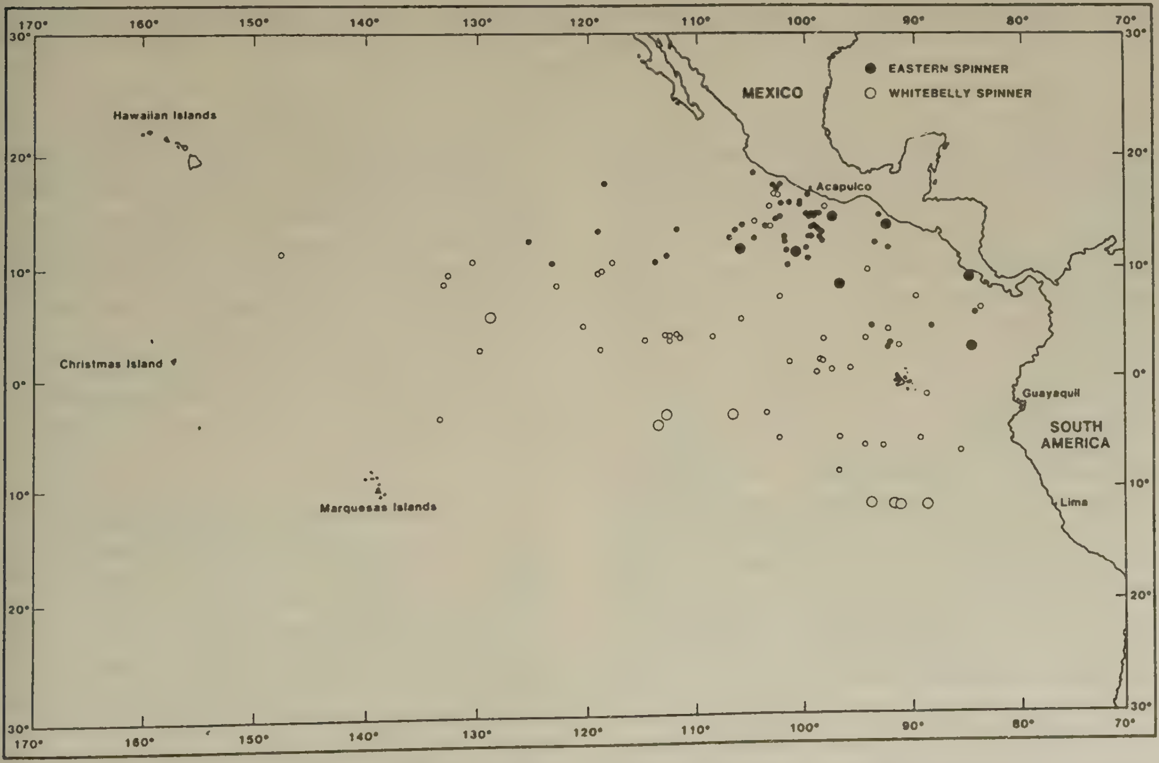

FIGURE 4.—Distribution of spinner dolphin schools, eastern and whitebelly forms, seen during the January-March research cruises. Larger circles indicate schools >300 animals.

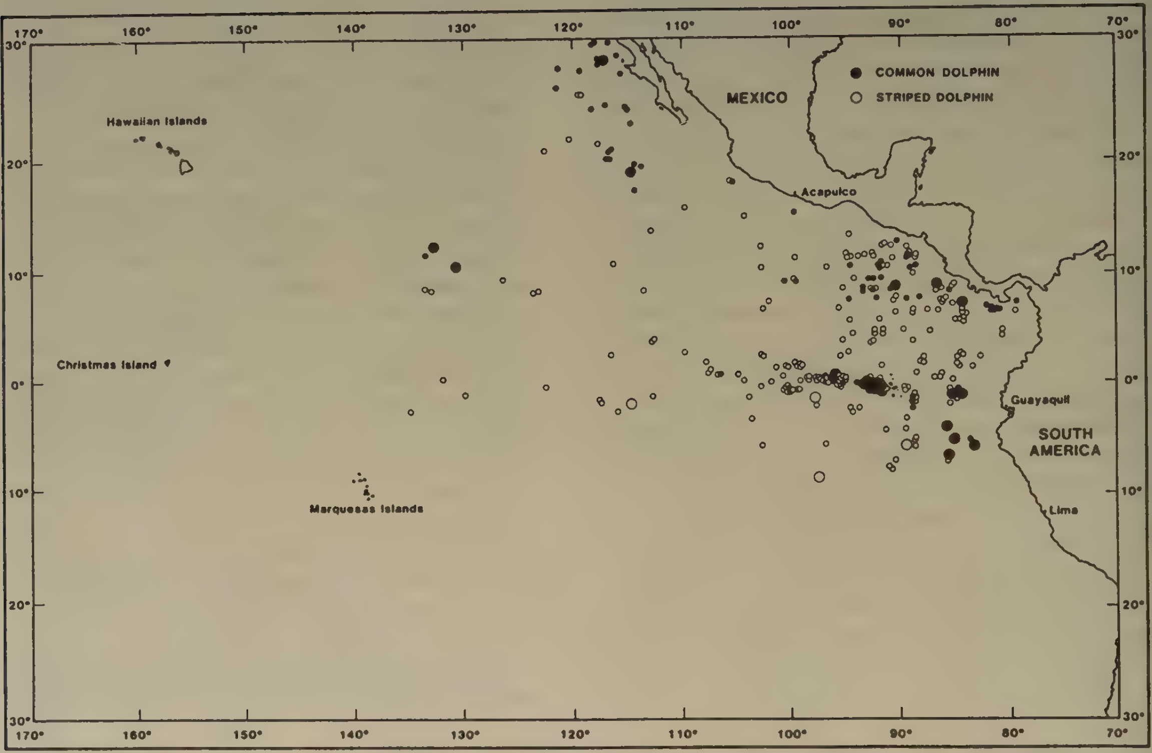

FIGURE 5.—Distribution of striped and common dolphin schools seen during the January-March research cruises. Larger circles indicate schools >300 animals.

distance searched during 1 d). Data for days during which the Beaufort wind force was equal to 4 (11-16 kn) for more than 50% of the time, or averaged more than 4, were not used. Only schools sighted at distances not more than 3 perpendicular nmi from the ship's track and not more than 5 radial nmi distant were considered, to reduce the effects due to distance on sightability. The latter criterion was not applied to the 1976 cruises, because the radial distances then were frequently overestimated. An areal smoothing procedure that consisted of calculating the average number of schools per 100 mi searched within sequential, overlapping 5° squares was employed. Sequential squares were offset 2.5° in latitude and longitude, so that each was wholly overlapped by 25% of the area of each of four adjacent squares. A day's sighting rate was assigned to a particular square if more than 50% of the search effort occurred therein, and the value was plotted at the center point of that square. If the search effort fell equally in two squares, the day's results were assigned to both squares. These moving, areal means of sightings per 100 nmi searched were plotted and contoured. Contouring (and interpolation) constituted a second level of areal smoothing.

The maps so generated describe the distribution of relative abundance of species schools as surveyed during January to March. These relative abundance data were combined for spotted and spinner dolphins and for striped and common dolphins, both because these species pairs had similar distributions and because pooling gave desirable sample sizes.

The combined spotted and spinner dolphin map (Fig. 6) shows some patterns already noted from the school distribution. These schools appeared relatively more abundant off southern Mexico (mostly spotted and eastern spinner dolphins) and again along an east-west band just north of the Equator, especially west of long. 105°W. Another band of greater abundance occurred south of the Equator. Spotted and spinner dolphins appeared less abundant just west of Costa Rica, off the coast of northern South America, and along the Equator. A weak lobe of higher relative abundance extended west of long. 120°W broadly about lat. 10°N.

Striped and common dolphins show a relative abundance pattern in which areas of higher density tend to be complementary to that of spotted and

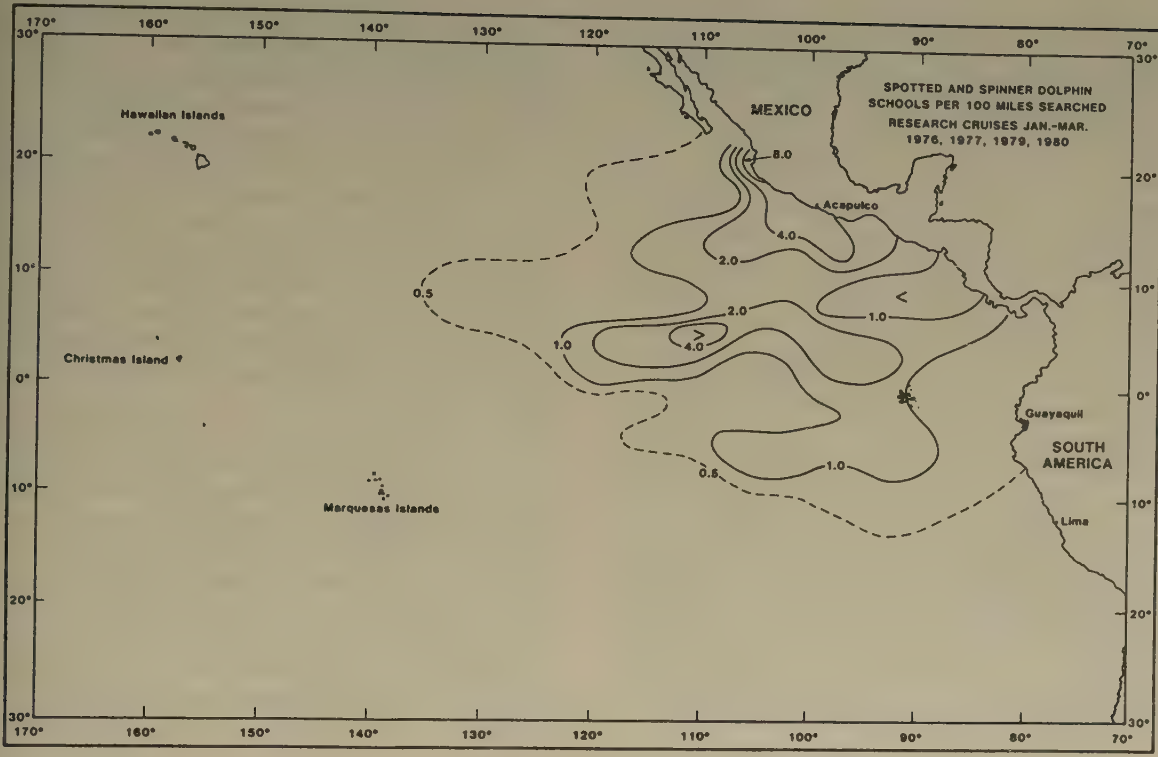

FIGURE 6.—Distribution of relative abundance of spotted and spinner dolphins, inferred from data of the January-March research cruises. Hawaiian and Marquesan sightings are not considered.

spinner dolphins (Fig. 7). Conspicuous lobes extended from off Baja California and also broadly from the coasts of Central America and northern South America out to and along the Equator. Within the latter lobe, centers of higher relative abundance occurred west of Nicaragua and Costa Rica and west of the Galapagos Islands, all areas where reduced abundance of spotted and spinner dolphins occurred. The Galapagos area and the lobe off Baja California were dominated by the common dolphin (cf. Fig. 5).

Dolphins of Tropical Water and Upwelling-Modified Water Habitats

The areas of greater frequency of spotted and spinner dolphins during January-March are the typical tropical waters of the eastern tropical Pacific. These waters are underlain by a sharp thermocline, generally >2°C/10 m, at depths usually much <50 m. The surface temperatures are >25°C, and the salinities <34‰. Such tropical waters are defined by Wyrtki (1966, 1967) as Tropical Surface Water (see Fig. 1). In particular the warm "Inner Tropical" Waters (Wyrtki 1964a) lying primarily north of the Equator comprise the major habitat of spotted and spinner dolphins (Fig. 6). The waters south of the Equator, where the relative abundance of these dolphins is also higher, are seasonally tropical, and are therefore called southern Subtropical Surface Water (Wyrtki 1966, 1967). These waters, occurring approximately south of lat. 2.5°S, have surface salinities >35‰, and during January-March (southern summer), warm to more than 26°C over a shallow, sharp thermocline. Since spotted and spinner dolphins occur there frequently, at least during January-March, it appears that spotted and spinner dolphins prefer all waters whose characteristics are, or become, tropical in the eastern Pacific. However the primary habitat appears to be the "Inner" Tropical Waters north of the Equator.

In contrast striped and common dolphins appear to prefer waters with more variable conditions during January-March. Their most important habitat appears to be broadly centered about equatorial waters (Fig. 7). This band of distribution extends into the central Pacific along the Equator. In the east it broadens widely to include Tropical Water off Central America and Subtropical Water off Peru. The equatorial distribution is in Equatorial Surface Water (Wyrtki 1966, 1967), a transitional water mass straddling the Equator and characterized by salinities between 34 and $35^0/_{00}$, upwelling, and a relatively weak thermocline. These waters are markedly cooled from June to December (southern winter-spring) by increased upwelling and by advection from the Peru Current. In the Subtropical Water habitats of striped and common dolphins, both off Peru and Baja California, there are also large seasonal changes in temperature structure and effects from upwelling. Finally the Tropical Water habitat in the Central American Bight is notably variable (below).

The waters we call the "Central American Bight" (roughly, the near coastal waters from Guatemala to Ecuador) constitute the most important area of overlap for spotted, spinner, striped, and common dolphins, but this overlap is not balanced among the species. These waters are tropical, but they are the most variable within the Tropical Surface Water province. The Equatorial Countercurrent, flowing eastward between lat. 4°N and 10°N, terminates and turns there, creating a complex circulation. The annual north-south migration in these latitudes of the Intertropical Convergence Zone, where north and south trade winds meet, bring southerly winds, rain, reduced salinity, and an intensified Countercurrent during the second half of the year (Bennett 1966; Wyrtki 1967, 1974; Forsebergh 1969). Later during the northern winter (January-March), northeasterly winds blow across Central America from the Atlantic, producing coastal upwelling, wind stirring, and more complex temperature patterns. The Costa Rica Dome, a localized, offshore upwelling at about lat. 8°N, long. 90°W (Wyrtki 1964b), also may be seasonally intensified (Hofmann et al. 1981).

These variable Central American Bight waters appear to have more abundant schools of striped and common dolphins than of spotted and spinner dolphins (cf. Figs. 3-7). It seems that all areas with greater concentration of striped and common dolphins have highly variable oceanographic features that are "upwelling-modified".

In spite of the rather strong overlap in distribution among the four dolphin species in the Central America Bight, the biogeographic distinction, including the relationships to environment, between

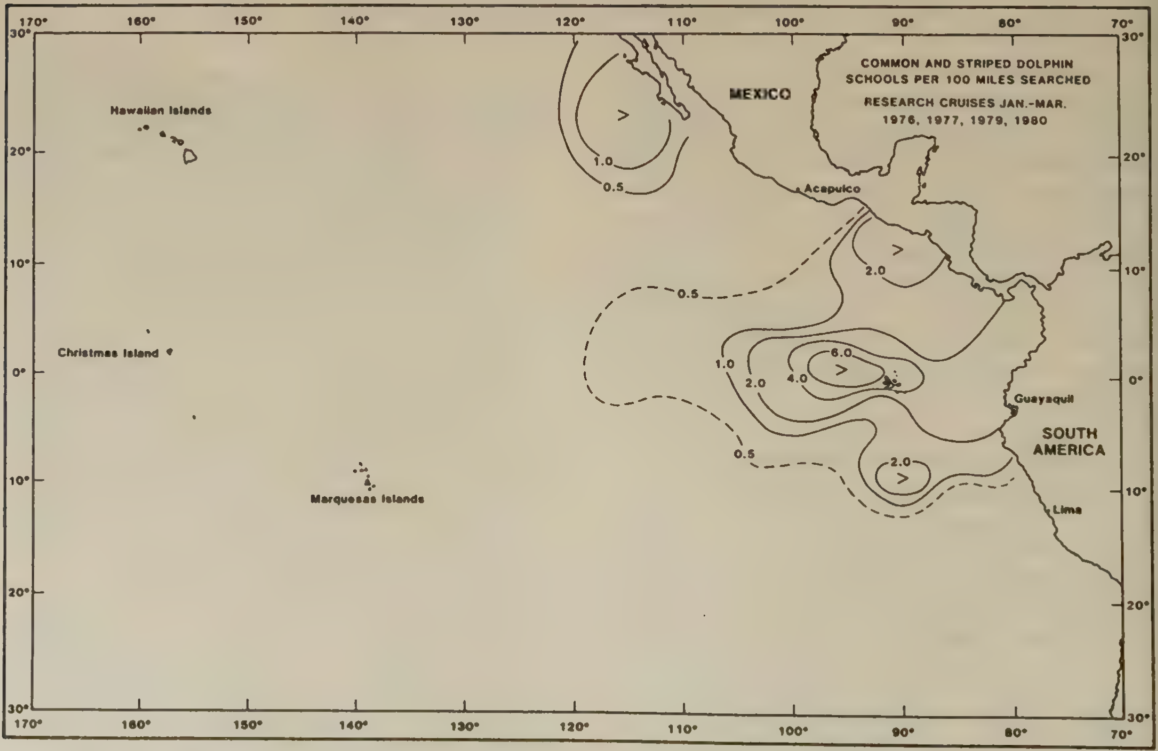
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FIGURE 7.—Distribution of relative abundance of striped and common dolphins, inferred from data of the January-March research cruises.

the spotted and spinner dolphins of the Tropical Water and the striped and common dolphins of the Upwelling-Modified Water may be quite apparent. This was the case during the intensive winter surveys of 1979 in the Central American Bight, shown in Figure 8. Superimposed in the figure are contours of the 20°C isotherm depth (essentially the thermocline depth) which were obtained from expendable bathythermograph probes dropped at 30-60 mi intervals (55.6-111.1 km). Notice that spotted and spinner dolphins were encountered mainly off southern Mexico, where the deeper 20°C isotherms indicated the occurrence of a large surface lens of warm water. The warmest surface waters in the eastern tropical Pacific normally occur in this area; the thermocline gradient is weaker, and the annual variation in surface temperature is relatively small (Wyrtki 1964a). In the more variable tropical waters of the Central American Bight, where the thermocline had shoaled or ridged to <60 m, both these species were seen too. However, striped and common dolphin schools predominated, especially near the shallower isotherms that mark the location of the Costa Rica Dome. Finally the equatorial distribution of primarily striped and common dolphins was evident. The sampling suggested that Subtropical Waters south of the Galapagos Islands were probably also important to these latter two species. A 1977 aerial survey of cetaceans in these waters off Central America (SWFC 1977[3]) obtained results similar to those just described.

Though there appear to be large-scale geographic differences in the habitats of spotted and spinner dolphins and of striped and common dolphins, there was no evidence of negative association among these species. The frequency of days in the Central American Bight, both in 1979 and 1980, with different combinations of these species encountered, are summarized in Table 2. There was no evidence, using chi-square contingency tests for association among spotted and/or spinner dolphins and striped or common dolphins, that the species were not occurring independently on any particular day.

Our contention that spotted and spinner dolphins and striped and common dolphins differentially inhabit waters of different oceanographic characteris-

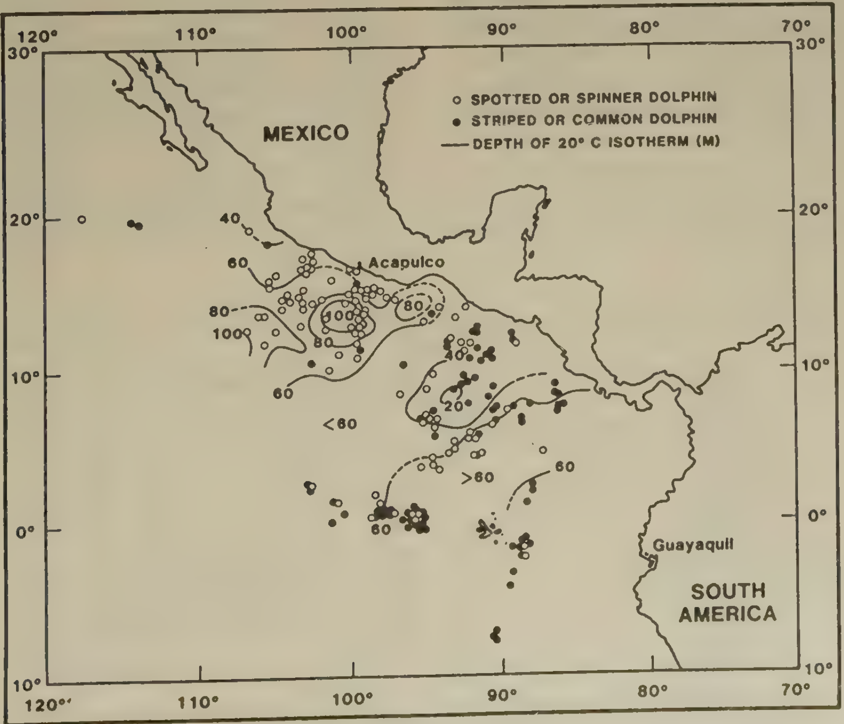

FIGURE 8.—Distribution of dolphin schools by species type in the Central American Bight, with reference to the depth of the 20°C isotherm. Data are from the January-March cruises of 1979.

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[3] Southwest Fisheries Center (SWFC). 1977. Aerial survey trip report January - June 1977. Admin. Rep. No. LJ-78-01, 73 p Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 2.—Number of days according to combinations of four species of dolphins that were encountered in the Central American Bight.

		Spotted and/or spinner				Striped		Common	
Year	Area[1]	Alone	With striped	With common	With striped + common	Alone	With common	Alone	None of these spp.
1979	N	17	2	0	0	1	1	1	6
	S	6	7	0	4	6	1	6	8
1980	N	9	2	0	0	0	0	0	0
	S	5	5	1	4	6	3	3	7

[1] Northern (N) and southern (S) areas are partitioned to illustrate species differences by area; the dividing line is perpendicular to the coast at lat. 16°N.

tics is supported by physical environmental measurements. The data indicated a species differential with respect to waters with temperature $\geqslant 25°$C and salinities $\leqslant 34.5‰$, and waters of $<25°$C and $>34.5‰$. The former is primarily Tropical Surface Water and the latter primarily Equatorial-Subtropical Surface Water. Of 217 spotted and/or spinner dolphin schools encountered during the January-March cruises, and having associated temperature and salinity measurements, 80.6% were in this Tropical Surface Water, while only 19.4% were in the Equatorial-Subtropical Surface Water. In comparison 53.7% of 229 similarly observed schools of striped and/or common dolphins were in the Tropical Surface Water and 46.3% were in the Equatorial-Subtropical Water. The differential in percentages by species pair reflects the more uniform "Inner Tropical" Surface Water habitat of spotted and spinner dolphins and the importance to striped and common dolphins of both the variable Tropical Water off Central America and the variable waters along the Equator, west of Peru, and southwest of Baja California.

Because the school sighting data are represented by many combinations of temperature and salinity from various areas, it is useful to summarize these results in terms of an integrated measure of temperature and salinity, i.e., sigma-*t*, a measure of water density (see Sverdrup et al. 1942). Table 3 lists the numbers and percentages of spotted and spinner and of striped and common dolphins according to their occurrence at different intervals of sigma-*t*. The percentages of striped and common dolphin schools were higher than that of spotted and spinner dolphin schools for sigma-*t* $\geqslant 22.5$ (primarily Equatorial-Subtropical Water). The opposite was true for sigma-*t* <22.5 (primarily Tropical Water). The difference in percentage distribution by species pair is significant ($P < 0.01$, Kolmogorov-Smirnov test).

Seasonal Features of Habitats

It is not clear how dolphin populations are affected by seasonal changes in the environment, although the available data suggest what may happen. The far offshore habitat of spotted and spinner dolphins, between long. 120°W and 140°W at about lat. 10°N, is an important "porpoise-tuna" fishing area during

TABLE 3.—Percent distribution of dolphin schools[1] according to surface water density (sigma-*t*).

sigma-*t*	Spotted	Spinner[2]	Total	%	Striped	Common	Total	%
+18.5-19.0					2		2	0.9
+19.0-19.5	2	1	3	1.4	5		5	2.2
+19.5-20.0	6		6	2.8	8		8	3.5
+20.0-20.5				0.0	2	1	3	1.3
+20.5-21.0	5	2	7	3.2	6	2	8	3.5
+21.0-21.5	16	12	28	12.9	11	2	13	5.7
+21.5-22.0	43	28	71	32.7	27	6	33	14.4
+22.0-22.5	12	32	54	24.9	26	19	45	19.7
+22.5-23.0	15	6	21	9.7	22	8	30	13.1
+23.0-23.5	8	11	19	8.8	39	15	54	23.6
+23.5-24.0	2	4	6	2.8	10	3	13	5.7
+24.0-24.5	2		2	0.9	6	6	12	5.2
+24.5-25.0					1	2	3	1.3
+25.0-25.5								
Total	111	96	217	100	165	64	229	100

[1] January-March, research cruises, 1976, 1977, 1979, 1980.
[2] Includes mixed spinner + spotted dolphin schools.

the spring and summer months (Calkins 1975). However there is little information from that area during the winter months (when there is little fishing), except for results from the January-March research cruises, which indicated that population densities there were not high (Fig. 6). This suggests a summer buildup in the concentration of these dolphins. This is likely because the offshore habitat is centered close to or along the divergence zone at the northern boundary of the North Equatorial Countercurrent, where the thermocline ridges and biological production is increased (Cromwell 1958). During the northern summer, the trade winds over the offshore habitat abate, ridging intensifies (Wyrtki 1964a, 1974), and porpoise-tuna fishing expands west of Clipperton Island (at ca. lat. 10°N, long. 109°W). The increase in fishing may be due to better weather, but possibly also to an increased abundance of dolphins and tuna.

The seasonal change in environment of the eastern tropical Pacific most likely to affect the distribution of dolphins is that due to the movement of the southern border of the tropical waters. During the northern winter, tropical conditions usually extend to about 15° south of the Galapagos Islands, when a shallow surface layer of warm water develops over what is actually Subtropical Water. During the northern summer, the cool Peru and South Equatorial Current strengthen, and a conspicuous thermal front, marking the southern boundary of Tropical Surface Water, usually develops. This Equatorial Front (Wyrtki 1966) is located a few degrees north of the Equator except for a short section east of the Galapagos Islands.

We studied the relationship of the Equatorial Front to dolphin populations during an October-November 1977 cruise of the *David Starr Jordan.* The Equatorial Front was conspicuous, as were the effects of the cool Peru and South Equatorial Currents (Fig. 9). Only 4 of 27 sightings of spotted and spinner dolphins schools in the equatorial region occurred in the cool, Equatorial and Subtropical Waters south of the front. The majority of the remaining 23 sightings were along the Equatorial Front, at the southern border to the warm Tropical Surface Water. These same species had occurred throughout these southern waters during January to March (Figs. 3, 4), when sea surface temperatures of 25°C or more prevailed over this entire area. The apparent redistribution of dolphin schools along the warm edge of the Peru Current and Equatorial Front appeared to be restricted to the spotted and spinner species, suggesting their seasonal movements away from cool southern waters. By implication these same dolphin species may migrate into southern waters during the warm season. Seasonal movements of dolphins (unidentified) in the southern waters is also suggested by results from the 1967 and 1968 EASTROPAC cruises (Love 1971, 1972). On the other hand, we did see during the October-November cruise four schools of spotted and spinner dolphins in cool Subtropical Water, and observers aboard tuna seiners have also reported these same species there during the cool season.

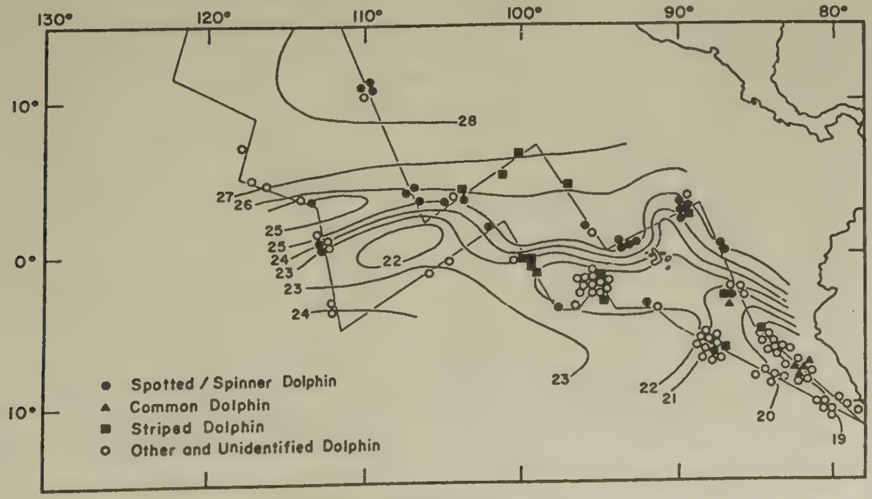

FIGURE 9.—Distribution of dolphin schools in the equatorial region during October-November 1977, relative to surface isotherms (°C). Notice the Equatorial Front or zone of rapid temperature change just north of the Equator. Clumping of sightings along the track is due to nighttime travel by ship. "Other" dolphins are primarily pilot whales.

Dolphin Communities

The habitat differences discussed also apply to other delphinid species, so that there seem to be different communities of dolphins in the eastern Pacific. To show how the cetacean communities differ between the habitats dominated by spotted and spinner and by striped and common dolphins, the eastern Pacific was divided into Areas I and II (Fig. 10, inset) that separate the main habitat areas of these two species pairs. Area I is primarily Tropical Surface Water and includes most areas where thermocline ridging is a dominant physical feature. Area II is primarily Equatorial-southern Subtropical Surface Water, but also includes the wedge-shaped area of variable Tropical Water in the Central American Bight. Area II comprises most of the waters we have called Upwelling-Modified.

In each of these two areas, only schools sighted at ≤1.0 nmi perpendicular to the ship's tracks were listed. This requirement was imposed so that percent species composition could be based on species schools, that to the largest practical degree, could all be sighted with equal probability, if present. The change in "sightability" with distance is different for each species because of differences in behavior, coloration, size, etc.

Our data indicate that the species composition of delphinids is different in these two areas. Percentage composition was determined for spotted; spinner; striped; common; bottlenose, *Tursiops truncatus*; rough-toothed, *Steno bredanensis*; and Risso's, *Grampus griseus*, dolphins, and for "blackfish", *Peponocephala electra/Feresa attenuata*; pilot whales, *Globicephala macrorhynchus*; and others (Table 4). Among 8 of 10 species-groups specifically identified in Table 4, there were significantly higher percentages of spotted, spinner, and rough-toothed dolphin schools in Area I than in Area II (Fig. 10). Risso's and bottlenose dolphins were important species in both areas, and their percentage values did not differ significantly between the areas. The percentages due to striped and common dolphins and pilot whales increased in Area II relative to Area I. Though reduced, the spotted dolphin remained important in the Area II dolphin community. The increase in percent composition of the common dolphin in Area II was not quite significant, reflecting the inclusion in Area I of that species' distributional lobe off Baja California. Overall, the species composition differed significantly between the two areas, as determined by chi-square contingency test of the frequency of species other than spotted, spinner, striped, and common, i.e., the species not initially considered when delimiting Areas I and II ($\chi^2 = 74.4$, df = 5, $P < 0.005$).

Additional evidence for the distinctiveness of the equatorial and subtropical portions of the Area II community is provided by observations along equatorial transects and transects south and south-

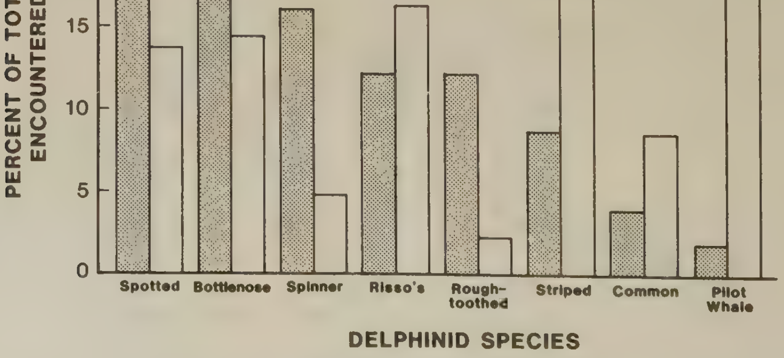

FIGURE 10.—Percent species composition of some important cetaceans, by Area I and II. See Table 4.

TABLE 4.—Percent composition of species as encountered in two areas[1] during the January-March research cruises.

Delphinid spp.[2]	Area I			Area II		
	Schools	%	95%[3] C.I.	Schools	%	95%[3] C.I.
Spotted, *Stenella attenuata*	67	24.7	19.6-29.8	55	13.2	10.0-16.4
Spinner, *Stenella longirostris*	41	15.1	10.8-19.4	19	4.6	2.6-6.6
Striped, *Stenella coeruleoalba*	22	8.1	4.9-11.3	86	20.6	16.7-24.5
Common, *Delphinus delphis*	10	3.7	1.5-5.9	34	8.2	5.6-10.8
Pilot whale, *Globicephala macrorhynchus*	5	1.8	0.2-3.4	75	18.0	14.3-21.7
Risso's, *Grampus griseus*	31	11.4	7.6-15.2	65	15.6	12.1-19.5
Bottlenose, *Tursiops truncatus*	50	18.5	13.9-23.1	58	13.9	10.6-17.2
Rough-toothed, *Steno bredanensis*	31	11.4	7.6-15.2	10	2.4	0.9-3.9
"Blackfish", *Peponocephala electra* or *Feresa attenuata*	8	3.0	1.0-5.0	1	0.2	0-0.6
Other	6	2.2	0.2-4.2	14	3.4	1.7-5.1
Total	271			417		

[1]Areas are shown in Figure 10.
[2]Species in mixed schools were tabulated separately.
[3]Normal approximation to binomial distribution.

east of the Galapagos Islands, i.e., off Peru. Unlike during the January-March cruises, physical oceanography was the primary task on most of these transects, hence the ships did not usually divert course toward the schools, and many schools could not be identified. Nevertheless some idea of the species compositions can be obtained. The observations (Table 5) showed that pilot whales and Risso's and bottlenose dolphins were frequently encountered species during October-December off Peru, and common dolphins were often seen near the coast. On the equatorial transects, between long. 85°W and 110°W, striped and common dolphins were the characteristic species. The common dolphin was seen most often near the Galapagos Islands. Pilot whales were relatively abundant during May-July 1981 in this equatorial section. West of long. 110°W along the Equator, pilot whales again were the most frequently encountered species. Interestingly, sightings of Fraser's dolphins, *Lagenodelphis hosei*, and "blackfish" (probably *Peponocephala electra*) were also relatively frequent, especially between long. 110°W and 145°W. These two species often school together and appear to prefer equatorial waters (Perryman et al.[4]). In the next section, another distinctive feature of equatorial waters will be brought out.

Dolphins, Birds, and Tuna

A conspicuous feature distinguishing the dolphin communities is the difference in the species-specific association with tunas. In the eastern tropical Pacific, spinner dolphins and especially spotted dolphins are found associated with "surface" yellowfin tuna. It is these two species, therefore, that are mainly affected by the porpoise-tuna fishery (Smith 1983). Surface tunas occur at the sea surface and can be caught by purse seine, trolling, and pole-and-line gear. "Deep tunas" of the same species are caught by longline gear, generally in and below the thermocline. Since these surface tunas drive food to the surface, making it available to certain seabirds (Ashmole and Ashmole 1957; Murphy and Shomura 1972), a reliable indication that tuna are accompanying a dolphin school is the presence of a bird flock. Birds are the most important cue used by fishermen to locate dolphin-tuna schools.

Birds do not occur equally among the different dolphin species. During the 1977, 1979, and 1980 January-March cruises (when the best bird observa-

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[4] Perryman, W. F., D. W. K. Au, and S. Leatherwood. Manuscr. prep. Melon-headed whale, *Peponocephala electra* (Gray, 1946) (with notes on the pygmy killer whale *Feresa attenuata*). Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 5.—Number of schools for species seen along equatorial and southeastern Pacific transects.

Region:	Off Peru: 0-10°S, 83° -95°W		Equator: 2°N-2°S 85° -110°W			Equator: 2°N-2°S 110° -145°W		Equator: 2°N-2°S 145° -180°W
Ships:	*D. S. Jordan*	*Researcher*	*Ocean-ographer*	*Researcher*	*Reseacher*	*Ocean-ographer*	*Ocean-ographer*	*Ocean-ographer*
Dolphin spp. Dates:	Oct.-Nov. 1977	Oct.-Dec. 1981	May-July 1981	July-Sept. 1980	Oct-Dec. 1981	Mar.-Apr. 1980	May-July 1981	Mar.-Apr. 1980
Unidentified	7	13	34	20	29	22	8	1
Spotted,								
Stenella attenuata	3	1	3	3		2	2	1
Spinner,								
S. longirostris	3		1	2		1	1	1
Striped,								
S. coeruleoalba	5	1	14	13	11	3	3	1
Common,								
Delphinus delphis	4	6	18	9	13			
Bottlenose,								
Tursiops truncatus	10	15	5	4	1		1	
Pilot,								
Globicephala macrorhynchus	14	9	14	4	3	16	5	7
Risso's,								
Grampus griseus	23	14	2		1	7		1
Rough-toothed,								
Steno bredanensis	1		1		1	4		1
Fraser's,								
Lagenodelphis hosei						7	1	1
"Blackfish",								
Peponocephala electra or *Feresa attenuata*	2		1			8		2
False killer whale,								
Pseudorca crassidens	1				1	1		2
Killer whale,								
Orsinus orca	1	1	1	2	3			

tions were taken), 70.7% of 167 spotted, spinner, or mixed spotted and spinner dolphin schools, sighted between lat. 5°N and 30°N (where most dolphin-tuna associations occur), had 10 or more associated birds (Table 6). We assume this minimum flock size indicates associated tuna, although we did not often actually see the tuna. For the same period and area, 30.6% of 49 common dolphin schools and only 1.6% of 64 striped dolphin schools were with 10 or more birds. The different percent occurrences indicate that tuna are most frequently associated with spotted and spinner dolphins and very seldom with the striped dolphin.

The bird species most numerous in offshore waters with dolphin schools are boobies (*Sula* spp.); wedge-tailed shearwaters, *Puffinus pacificus*; and sooty terns, *Sterna fuscata*. Frigate birds (*Fregata* spp.) are also closely associated with these dolphins, though their average flock size is only seven (Au and Pitman[5]). These bird species are all strongly dependent upon tunas in their feeding. Our observations are that the birds feed primarily in association with the fish, not the dolphins.

The dolphin-tuna-bird association appears to be area- as well as species-specific. Assuming flocks of ⩾10 birds indicate the presence of yellowfin tuna, this association seems to occur in all areas with higher relative abundance of spotted and spinner dolphins (Fig. 11). The association seldom occurs along the Equator, or in areas outside the traditional porpoise-tuna fishing grounds (roughly these are waters within the triangular-shaped area whose base is formed by the American coasts between lat. 25°N and 15°S, and whose apex is at lat. 10°N, long. 150°W; see Calkins 1975 and IATTC 1979-81), even though the required species of dolphins, tuna, and birds may be present there. Relatively few of the spotted or spinner dolphin schools sighted near the Equator were with bird flocks. South of the Equator and in the Central Pacific, there are abundant flocks of sooty terns with fish schools, but dolphins do not usually co-occur (Au and Pitman fn. 5). The most important area of the dolphin-tuna-bird association is centered about the divergence zone near lat. 10°N, an important porpoise-tuna fishing ground for yellowfin tuna (primarily Area I of Figure 10).

These areal changes in the interactions among species are usually clearly apparent during north-south transects across the eastern Pacific during any season. An example is the July-September 1980, NOAA ship *Researcher* transits between Manzanillo, Mexico, and lat. 3°S, long. 100°W, via Clipperton Island. At that time Tropical Surface Water (T > 25°C) extended to the Equator with transition toward Equatorial Water marked by temperature and salinity fronts at lat. 5°N-6°N and at the Equator (Fig. 12). In the tropical waters north of the front at lat. 5°N there was a conspicuous increase in abundance of flocks of sooty terns, boobies, and shearwaters (*Puffinus* spp.), all broadly centered about the thermocline ridge at lat. 10°N. The larger gadfly petrels (*Pterodroma* spp.) were also abundant. All of these birds frequently flock over fish and dolphins. South of this boundary was another avian group, with *Pterodroma leucoptera*, a small petrel from the Southern Hemisphere, and planktivorous storm petrels (*Oceanodroma* spp.) predominating, and peak abundances at the Equator. These latter birds usually feed independently of fish and seldom flock over fish and dolphins.

Correlations among water masses, seabirds, and the different cetaceans along the transect were difficult to quantify because of the small sample size of the latter. However, the observations are supportive of such relationships. There were 39 dolphin schools, of which 15 were unidentified, and 21 whale schools along this transect. Spotted and spinner

TABLE 6.—Dolphin schools associated with seabirds.

	5°N-30°N			<5°N		
Dolphin spp.	Schools	with ⩾10 birds	%	Schools	with ⩾10 birds	%
Spotted	95	56	58.9	40	8	20.0
Spotted and spinner	55	53	96.4	21	8	38.1
Spinner	17	9	52.9	19	6	31.6
Common	49	15	30.6	10	1	10.0
Striped	64	1	1.6	76	1	1.3
Rough-toothed	40	5	12.5	13	1	7.7
Other/unidentified	388	17	4.4	189	6	3.2

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[5] Au, D. W. K., and R. L. Pitman. Manuscr. prep. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

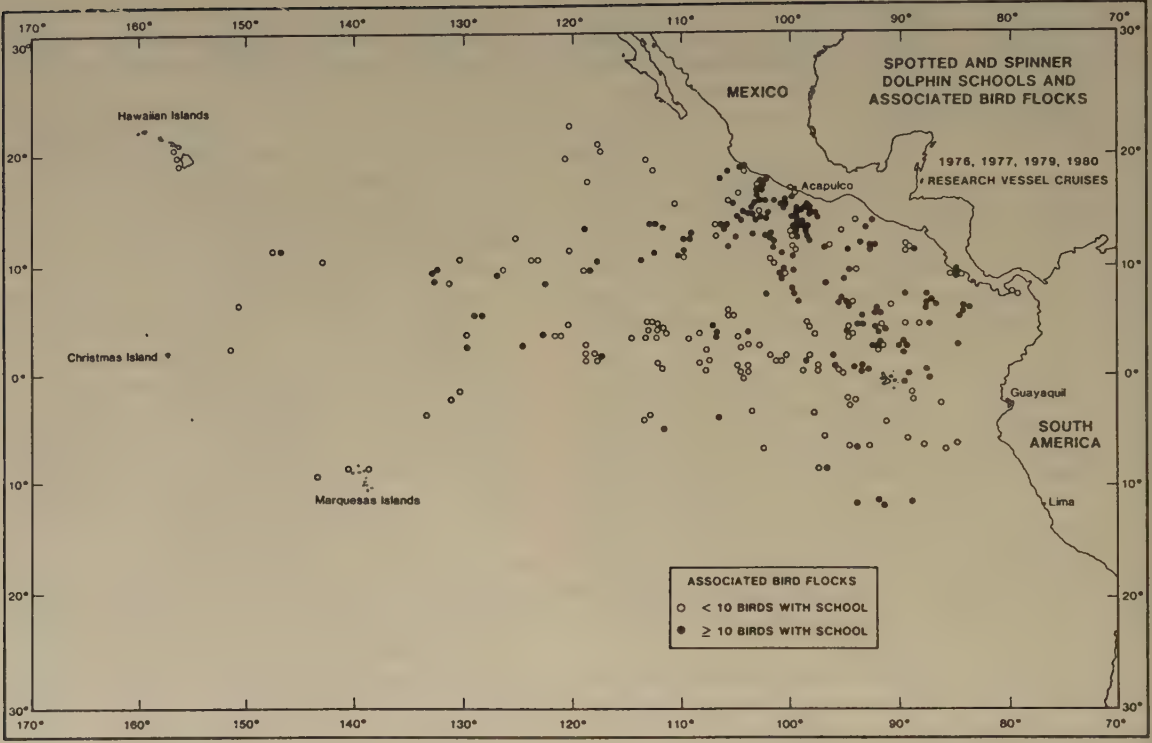
SPOTTED AND SPINNER DOLPHIN SCHOOLS AND ASSOCIATED BIRD FLOCKS
1976, 1977, 1979, 1980 RESEARCH VESSEL CRUISES
MEXICO
Acapulco
Hawaiian Islands
Christmas Island
Marquesas Islands
Guayaquil
SOUTH AMERICA
Lima
ASSOCIATED BIRD FLOCKS
○ < 10 BIRDS WITH SCHOOL
● ≥ 10 BIRDS WITH SCHOOL
170° 160° 150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20° 30°

FIGURE 11.—Distribution of bird-associated spotted and spinner dolphin schools during the January-March research cruises. Schools with 10 or more birds are assumed to be with tuna.

dolphns did occur coincidentally with bird flocks (and probably with tuna) in the warmer tropical waters centered about lat. 10°N, but also were seen at the Equator, though without associated bird flocks. Striped and common dolphins occurred in coastal and equatorial waters, without bird flocks. These latter dolphins were the characteristic species on the equatorial transect of this same cruise (see Table 5, col. 4), where only one of the schools seen, a mixed spotted and spinner dolphin school, had an associated bird flock. The distinct change in the bird fauna south of lat. 5°N to species that do not forage commensally with fish suggests there are changes with water masses in the nature of epipelagic prey and how the top predators forage.

DISCUSSION

It should not be surprising that the two major divergence zones of the eastern Pacific, near lat. 10°N and along the Equator, are important features of the oceanic habitats of eastern Pacific cetaceans. Enriched by the effects of wind and the major zonal currents (Brandhorst 1958; Cromwell 1958; Reid 1962; Wyrtki 1966), the zones are evident areas of enhanced biological production (Blackburn 1966, 1976; Blackburn et al. 1970; King 1974; Parsons et al. 1977; Brinton 1979). that are important to tunas (Calkins 1975; Blackburn 1965; Blackburn and Laurs 1972; Blackburn and Williams 1975; Sund 1981) and cetaceans as discussed above. These two zones are not qualitatively the same, however; the strong, shallow thermoclines that have been related to successful porpoise-tuna fishing (Green 1967; Miller et al.[6]) and to aggregations of dolphins and baleen whales (Rovnin 1969; Volkov and Moroz 1976) are characteristic of the lat. 10°N zone, but not of the Equator. Similarly the oxygen minimum layer, noted by Perrin et al. (1976) to be correlated with the distribution of the spotted dolphin, occurs only north and south of the Equator in the eastern Pacific. Equatorial waters are characterized by shallow, weak (<2°C/10 m) thermoclines, due to upwelling and the Equatorial Undercurrent, and cool surface temper-

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[6] Miller, F. R., C. J. Orange, R. H. Evans, and K. A. Bliss. Manuscr. prep. Analysis of environment related to tuna fishing in ETP. Inter-American Tropical Tuna Commission, La Jolla, CA 92038.

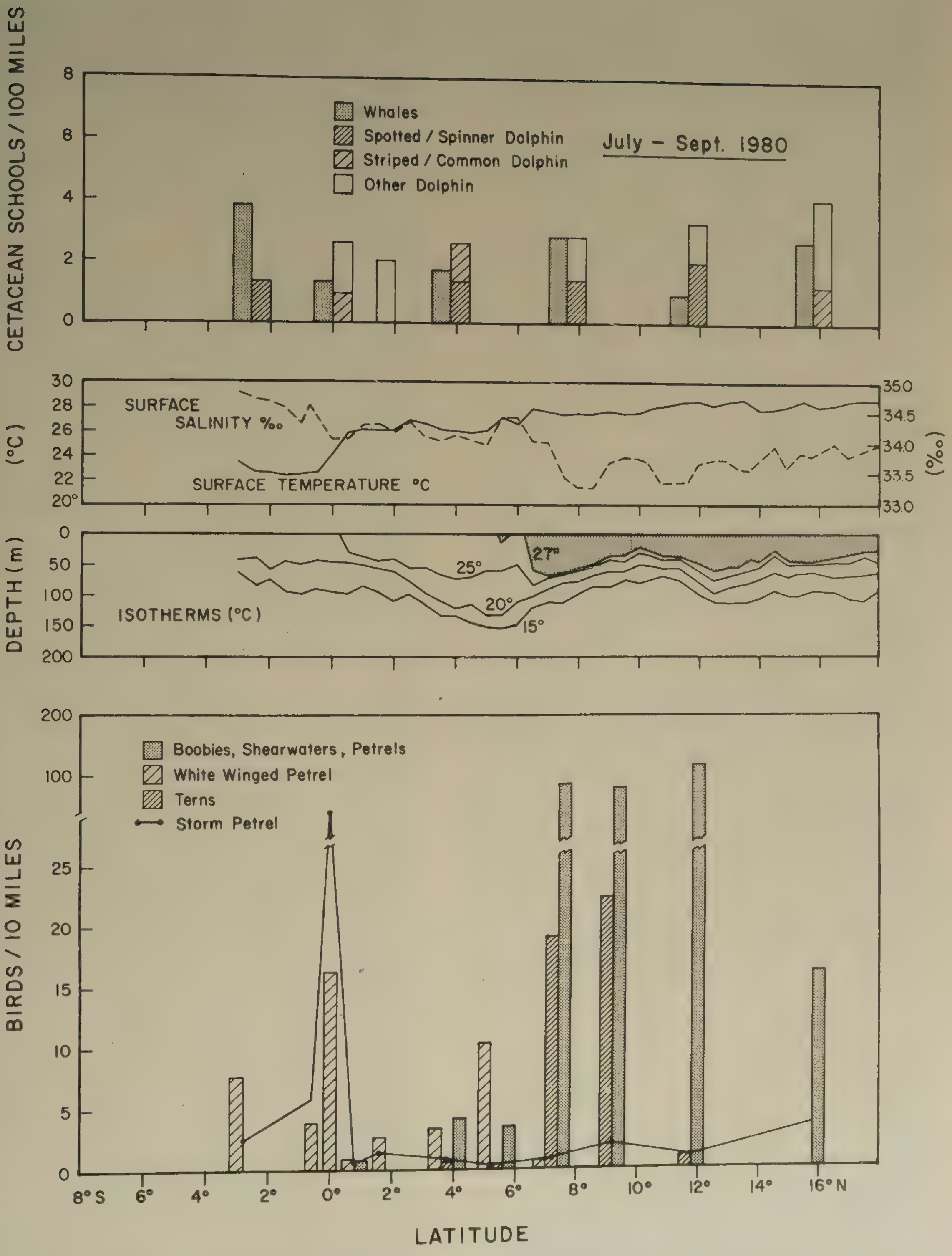

FIGURE 12.–Transect along long. 110°W, July-September 1980, showing changes in cetaceans, birds, and temperature and salinity. The relative abundance of dolphin schools include unidentified schools which were prorated according to species ratios of identified schools.

ature from June through December. These waters support a different cetacean community (Table 5), though school densities there can be as high as in areas off Mexico and Central America (Au et al. 1980).

Other relationships between distribution and movements of dolphins and water masses, convergences, and thermal conditions have been described by Fraser (1934), Gaskin (1968), Kasuya (1971), Nishiwaki (1975), Evans (1975), and Miyazaki and Nishiwaki (1978). Hui (1979) found that common dolphins off California tended to occur over prominent features of bottom topography. The deep depths of such areas suggest that surface eddies and convergences caused by topography-induced accelerations to deep reaching currents (Sverdrup et al. 1942; Neumann 1960) may have concentrated food and attracted the dolphins.

The distributions of dolphin species as seen from the January-March cruises (Figs. 3-7) are similar to the all-season school distributions derived from data of scientific observers aboard tuna seiners. These data, consisting of thousands of sightings per species, were recently summarized by Scott (1981) and Perrin et al. (1983). The same major distributional patterns as presented here for the January-March cruises were apparent, including, for spotted and spinner dolphins, the relative unimportance of equatorial latitudes and the secondary band of increased concentration of schools 2°-5° north of the Equator. The latter may be related to the Equatorial Front and increased food concentration and possibly production in the convergence zone there (Sette 1955; King and Iverson 1962; Blackburn and Laurs 1972; Murphy and Shomura 1972; Pak and Zaneveld 1974; Blackburn and Williams 1975; Greenblatt 1979). Increased abundance of micronekton occurs at least sometime in this zone (Love 1971, 1972; Blackburn and Laurs 1972). The purse seiner data, like those of this paper also showed spotted and spinner dolphins more concentrated in the tropical waters off Mexico and along lat. 10°N, while striped and common dolphins tended to be found in the Central American Bight and along the Equator. This complementary type of distribution was less apparent with the more broadly distributed striped dolphin. It should be noted that our southern distributional lobe for spotted and spinner dolphins, at ca. lat. 5°S, may in part be due to the sampling pattern. However, the density of these dolphins along the Equator is definitely reduced, and we know of no information that does not suggest a rapid decline in density south of our lobe.

Our January-March data differs from the all-season data in indicating fewer schools in the area around the Revilla Gigedo Islands (at ca. lat. 19°N, long. 111°W) and between long. 90°W and 100°W along lat. 10°N for spotted and spinner dolphins. Also our data suggested that striped and common dolphins had a more localized distribution near the region of the Costa Rica Dome, and were relatively infrequent between long. 105°W and 120°W, along lat. 10°N. These differences may be due to seasonal changes in distribution.

The relative densities of these dolphins, as school encounter rates in the tuna purse seine fishery, were recently calculated by Polacheck (1983). The patterns he derived were fragmentary, but not inconsistent with those of this paper. He showed, for example, higher densities of spotted and spinner dolphins extending to the southwest from off southern Mexico and reduced densities in the Central American Bight. For striped and common dolphins, he also described a three-lobed distribution pattern as in this paper. However his equatorial lobe was centered just south of the Equator.

It seems likely that the dolphin community of the Upwelling-Modified Water differs from the Tropical Water community because of water-mass specific differences in the distribution and availability of food. This is supported by the different biotic features of Equatorial and Subtropical Waters relative to Tropical Waters. The distinction is clearly shown by the surface distribution of nutrients and primary production in these waters as measured during the EASTROPAC cruises (Love 1971, 1972). The equatorial waters of the eastern Pacific in particular are different. They support abundant plankton-feeding storm petrels rather than fish and cephalopod-feeding flocking birds that are usually abundant both north and south of the Equator (see also Love 1971, 1972 and King 1974). Dolphin species along the Equator tend not to be with fish or birds (Figs. 11, 12), and the species composition of the cetacean community appears to be distinct (Table 5; Au and Pitman 1981). Of course it has previously been known that equatorial waters are notable in being important sperm whale grounds (Townsend 1935) and have a zooplankton community distinct from other parts of the eastern tropical Pacific (McGowan 1972). Finally the fact that the common dolphin, a species characteristic of coastal upwelling waters from California to Peru, occurs with greater frequency in the equatorial waters and near upwelling areas in the Central American Bight, suggests that the shorter and different food chains of the upwelling environments (Parsons et al. 1977) may be the basis of the community difference.

The dolphin-tuna-bird association is one manifestation of community difference that is both striking and of ecological interest. The distribution of this association is notable in that it seems coincident with both the main habitats of spotted and spinner dolphins and the distribution of "surface" yellowfin tuna in the eastern Pacific (see Figure 11, Shingu et al. 1974, and Suzuki et al. 1978). Since it is primarily these dolphins that are associated with birds and with yellowfin tuna, the geography of the dolphin-bird association also defines that of the dolphin-yellowfin tuna association. This association of birds and fish with dolphins occurs in all tropical waters, including the southern Subtropical Water during the southern summer. It is apparently rare in equatorial waters of the eastern Pacific, in the central and western Pacific (Myazaki and Wada 1978; Au et al. fn. 2), and in the eastern tropical Atlantic (Levenez et al. 1980). In the central Pacific the same bird species found with spotted and spinner dolphins in the eastern tropical Pacific can be abundant (Gould 1974), and sooty terns especially, are frequently associated with small tunas, but these are most likely skipjack tuna (Murphy and Ikehara 1955; Waldrom 1964; Hida 1970; Blackburn and William 1975). Apparently those flocks seldom accompany dolphins or schools of larger yellowfin tuna. Yellowfin tuna and dolphins seldom seem to associate outside the eastern tropical Pacific.

The obvious feeding activity often seen in these joint aggregations of birds, spotted and spinner dolphins, and tuna suggests that these species have similar food and foraging requirements. Our observations indicate that the mammals and fish are not tightly associated in the aggregations (see Au and Perryman 1982) and probably feed independently (see also Norris and Dohl 1980a). However the tuna, birds, and spotted dolphin (at least) do appear to be feeding at the same time. Both the tuna and spotted dolphins feed on epipelagic fish and on squids (Perrin et al. 1973; Olson 1982), but the spinner dolphins feed differently and may forage more at night (Perrin et al. 1973; Norris and Dohl 1980b); though they are active in these feeding aggregations, they may not be directly associated with the tuna. Judging from the associations of bird and dolphin species, only spotted and spinner dolphins frequently find it advantageous to feed with yellowfin tuna. Furthermore the distribution of this association suggests that the necessary kind and behavior of prey that is likely the basis of the association appears characteristic of tropical, but not equatorial, waters. It occurs especially where a shallow thermocline may constrain the yellowfin tuna to the surface layer with the dolphins, a complex interaction between environment and physiology (Sharp 1978) that may cause the phenomenon known as "surface tuna". Finally the distribution of the bird-dolphin association indicates that the dolphin-tuna association is characteristic of areas of higher school density of spotted and spinner dolphins. High population densities of both dolphins and yellowfin tuna, and suitable prey are therefore likely requisites for joint dolphin-tuna schools. The dolphin-tuna association is a feature of the most productive tuna fishing zones of these tropical seas. In such rich areas, feeding tactics to exploit clumped prey could lead to multispecies aggregations of predators, as explained by Schoener (1982).

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LITERATURE CITED

ALVERSON, F. G.
1981. Comments on the distribution of spotted, spinner, common and striped dolphin in the tropical Pacific Ocean. *In* P. S. Hammond (editor), Report on the Workshop on Tuna-Dolphin Interactions, p. 109-124. Inter-Am. Trop. Tuna Comm., Spec. Rep. 4, App. 5.

ASHMOLE, N. P., AND M. J. ASHMOLE.
1957. Comparative feeding ecology of seabirds of a tropical oceanic island. Yale Univ. Peabody Mus. Nat. Hist. Bull. 24:1-131.

AU, D. W., W. L. PERRYMAN, R. L. PITMAN, AND M. S. SINCLAIR.
1980. Cetacean populations and equatorial oceanography. Trop. Ocean Atmos. Newsl., Univ. Wash., 4:6-10.

AU, D. W. K., AND R. L. PITMAN.
1981. The equatorial cetacean community of the eastern Pacific. (Abstr.) Proceedings of the Fourth Biennial Conference on the Biology of Marine Mammals, Dec. 14-18, 1981, p. 95.

AU, D., AND W. PERRYMAN.
1982. Movement and speed of dolphin schools responding to an approaching ship. Fish. Bull., U.S. 80:371-379.

BENNETT, E. B.
1966. Monthly charts of surface salinity in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 11:3-44.

BLACKBURN, M.
1965. Oceanography and the ecology of tunas. Oceanogr. Mar. Biol. Annu. Rev. 3:299-322.
1966. Biological oceanography of the eastern tropical Pacific: summary of existing information. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 540, 18 p.
1976. Review of existing information on fishes in the deep ocean mining environment study (DOMES) area of the tropical Pacific. Inst. Mar. Res., Univ. Calif., IMR NO. 76-1, 77 p.

BLACKBURN, M., AND R. M. LAURS.
1972. Distribution of forage of skipjack tuna (*Euthynnus pelamis*) in the eastern tropical Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-649, 16 p.

BLACKBURN, M., R. M. LAURS, R. S. OWEN, AND B. ZEITSCHEL.
1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton, and micronekton in the eastern tropical Pacific. Mar. Biol. (Berl.) 7:14-31.

BLACKBURN, M., AND F. WILLIAMS.
1975. Distribution and ecology of skipjack tuna, *Katsuwonus pelamis*, in an offshore area of the eastern tropical Pacific Ocean. Fish. Bull., U.S. 73:382-411.

BRANDHORST, W.
1958. Thermocline topography, zooplankton standing crop, and mechanisms of fertilization in the eastern tropical Pacific. J. Cons. Int. Explor. Mer 24:16-31.

BRINTON, E.
1979. Parameters relating to the distribution of planktonic organisms, especially euphausiids in the eastern tropical Pacific. Prog. Oceanogr. 8:125-189.

CALKINS, T. P.
1975. Geographical distribution of yellowfin and skipjack tuna catches in the eastern Pacific Ocean, and fleet and total catch statistics, 1971-1974. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 17:3-116.

CROMWELL, T.
1958. Thermocline topography, horizontal currents and "ridging" in the eastern tropical Pacific. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 3:135-164.

EVANS, W. E.
1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. Thesis, Univ. California, Los Angeles, 164 p.

FORSBERGH, E. D.
1969. On the climatology, oceanography, and fisheries of the Panama Bight. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 14:45-385.

FRASER, F. C.
1934. Report on cetacea stranded in British coasts from 1927 to 1932. Br. Mus. (Nat. Hist.) No. 11, 41 p.

GASKIN, D. E.
1968. Distribution of delphinidae (Cetacea) in relation to sea surface temperature off eastern and southern New Zealand. N.Z. J. Mar. Freshw. Res. 2:527-534.

GOULD, P. J.
1974. Sooty tern (*Sterna fuscata*). *In* W. B. King (editor), Pelagic studies of seabirds in the central and eastern Pacific Ocean, p. 6-52. Smithson. Contrib. Zool. No. 158.

GREEN, R. E.
1967. Relationship of the thermocline to success of purse seining for tuna. Trans. Am. Fish. Soc. 96:126-130.

GREENBLATT, P. R.
1979. Associations of tuna with flotsam in the eastern tropical Pacific. Fish. Bull., U.S. 77:147-155.

HIDA, T. S.
1970. Surface tuna schools located and fished in equatorial eastern Pacific. Commer. Fish. Rev. 32(4):34-37.

HOFMANN, E. E., A. J. BUSALACCHI, AND J. J. O'BRIEN.
1981. Wind generation of the Costa Rica Dome. Science (Wash., D.C.) 214:552-554.

HUI, C. A.
1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California Bight. J. Mammal. 60:521-527.

INTER-AMERICAN TROPICAL TUNA COMMISSION.
1979. Annual report of the Inter-American Tropical Tuna Commission. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, CA.
1980. Annual report of the Inter-American Tropical Tuna Commission. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, CA.
1981. Annual report of the Inter-American Tropical Tuna Commission. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, CA.

KASUYA, T.
1971. Consideration of distribution and migration of toothed whales of the Pacific coast of Japan based upon aerial sighting record. Sci. Rep. Whales Res. Inst. 23:37-60.

KING, J. E., AND R. T. B. IVERSON.
1962. Midwater trawling for forage organisms in the central Pacific 1951-1956. U.S. Fish Wildl. Serv., Fish. Bull. 62: 271-321.

KING, W. B. (editor).
1974. Pelagic studies of seabirds in the central and eastern Pacific Ocean. Smithson. Contrib. Zool. No. 158, 277 p.

LEVENEZ, J., A. FONTENEAU, AND R. REGALADO.
1980. Resultats d'une enquete sur l'importance des dauphins dans la pecherie thoniere FISM. Int. Comm. Conserv. Atl. Tunas, Coll. Vol. Sci. Pap. IX(1):176-179.

LOVE, C. M. (editor).
1971. Biological and nutrient chemistry data from principal participating ships, first survey cruise, February-March 1967. EASTROPAC Atlas, Vol. 2. Natl. Mar. Fish. Serv., Circ. 330, 87 p.
1972. Biological and nutrient chemistry data from principal participating ships, second survey cruise, August-September 1967. EASTROPAC Atlas, Vol. 6. Natl. Mar. Fish. Serv., Circ. 330, 80 p.

MCGOWAN, J. A.
1972. The nature of oceanic ecosystems. *In* C. B. Miller (editor), The biology of the oceanic Pacific, p. 9-28. Proc. 33d Annu. Biol. Colloq., Oreg. State Univ. Press, Corvallis, OR.

MIYAZAKI, N., AND M. NISHIWAKI.
1978. School structure of the striped dolphin off the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. 30:65-115.

MIYAZAKI, N., AND S. WADA.
1978. Observations of cetacea during whale marking cruise in the western tropical Pacific 1976. Sci. Rep. Whales Res. Inst. 30:179-195.

MURPHY, G. I., AND I. I. IKEHARA.
1955. A summary of sightings of fish schools and bird flocks and of trolling in the central Pacific. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 154, 19 p.

MURPHY, G. I., AND R. S. SHOMURA.
1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. Fish. Bull., U.S. 70:875-913.

NEUMANN, G.
1960. On the effect of bottom topography on ocean currents. Dtsch. Hydrogr. Z., 13:132-141.

NISHIWAKI, M.
1975. Ecological aspects of smaller cetaceans, with emphasis on the striped dolphin (*Stenella coeruleoalba*). J. Fish. Res. Board Can. 32:1069-1072.

NORRIS, K. S., AND T. D. DOHL.
1980a. The structure and functions of cetacean schools. *In* L. M. Herman (editor), Cetacean behavior, mechanisms and functions, p. 211-261. John Wiley and Sons, N.Y.
1980b. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish. Bull., U.S. 77:821-849.

OLSON, R. J.
1982. Feeding and energetic studies of yellowfin tuna, food for ecological thought. Coll. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas XVII(2):444-457.

PARSONS, T. R., M. TAKAHASHI, AND M. HARGRAVE.
1977. Biological oceanographic processes. Pergamon Press, N.Y., 332 p.

PAK, H., AND J. R. V. ZANEVELD.
1974. Equatorial front in the eastern Pacific Ocean. J. Phys. Oceanogr. 4:570-578.

PERRIN, W. F.
1975a. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. J. Fish. Res. Board Can. 32:1059-1067.
1975b. Variation of the spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. Bull. Scripps Inst. Oceanogr. 21, 206 p.

PERRIN, W. F., J. M. COE, AND J. R. ZWEIFEL.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

PERRIN, W. F., D. B. HOLTS, AND R. B. MILLER.
1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75:725-750.

PERRIN, W. F., G. J. WALKER, F. M. RALSTON, AND D. W. K. AU.
1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific with an annotated catalog of data sources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-38, 65 p.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

POLACHECK, T.
1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tuna purse seiners. Ph.D. Thesis, Univ. Oregon, Eugene, 475 p.

REID, J. L., JR.
1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7:287-306.

ROVNIN, A. A.
1969. Distribution of true whales in the tropical part of the Pacific. *In* V. A. Arseniev, B. A. Zenkovich, K. K. Chapsky (editors), Transactions of the Third All-Union Conference on Marine Mammals, p. 144-149. Nauka, Moskva, U.S.S.R.

SCHOENER, T. W.
1982. The controversy over interspecific competition. Am. Sci. 70:586-595.

SCOTT, M. D.
1981. Dolphin stocks in the eastern tropical Pacific. *In* P. S. Hammond (editor), Report on the workshop on tuna-dolphin interactions, p. 98-107. Inter-Am. Trop. Tuna Comm. Spec. Rep. No. 4, App. 4.

SETTE, O. E.
1955. Consideration of midocean fish production as related to oceanic circulatory systems. J. Mar. Res. 14:398-414.

SHARP, G. D.
1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 397-449. Acad. Press, N.Y.

SHINGU, C., P. K. TOMLINSON, AND C. L. PETERSON.
1974. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1967-1970. [In Engl. and Span.] Bull. Inter-Am. Trop. Tuna Comm. 16:67-230.

SMITH, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull., U.S. 81:1-13.

SUND, P. N., M. BLACKBURN, AND F. WILLIAMS.
1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr. Mar. Biol. Annu. Rev. 19:443-512.

SUZUKI, Z., P. K. TOMLINSON, AND M. HONMA.
1978. Population structure of Pacific yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull., 17:277-358.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans, their physics, chemistry, and general biology. Prentice-Hall, Inc., N.Y., 1087 p.

TOWNSEND, C. H.
1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica 19:1-50.

VOLKOV, A. F., AND I. F. MOROZ.
1976. Oceanological conditions of the distribution of cetacea in the eastern tropical part of the Pacific Ocean. Int. Whaling Comm. Rep. 27:186-188.

WALDRON, K. D.
1964. Fish schools and bird flocks in the central Pacific Ocean, 1950-1961. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 464, 20 p.

WYRTKI, K.
1964a. The thermal structure of the eastern Pacific Ocean. Erganzungsh. Dtsch. Hydrogr. Z. Reiche A 8(6), 84 p.
1964b. Upwelling in the Costa Rica Dome. U.S. Fish Wildl. Serv., Fish. Bull., 63:355-372.
1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Annu. Rev. 4:36-68.
1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1:117-147.
1974. Equatorial currents in the Pacific 1950 to 1970 and their relations to the trade winds. J. Phys. Oceanogr. 4:372-380.

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COMPARATIVE STUDIES AND THE RECRUITMENT PROBLEM: SEARCHING FOR GENERALIZATIONS

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ABSTRACT

Empirical attempts to relate recruitment variation to variability in the environment or in the biological community have not been notably successful. This is due in part to the very short data series generally available for empirical analysis. Obviously, we must develop generalizations to provide a basis for unifying the available fragments of experience in a coherent framework.

The ecosystems of the four major subtropical eastern ocean boundary regions, i.e., the California, Peru, Canary, and Benguela current regions, appear to be controlled by similar environmental dynamics (characteristic late spring distributions of coastal temperature anomaly and Ekman transport for the four regional systems, supplementing previously reported winter and summer distributions, are presented). These regions contain very similar assemblages of exploitable pelagic fishes, and exhibit comparable histories of fishery growth and abrupt decline. The similarities suggest that fish communities in these different systems may function alike with respect to their environments and may have reproductive strategies for similar environmental problems. Because natural selection implies that reproductive strategies are responses to the most crucial factors regulating reproductive success, compelling patterns of correspondence among reproductive habits and environmental characteristics are likely to reflect important causal mechanisms. Such findings, which are independent of time series results, furnish a guide for selecting variables for time series modeling in a way that makes improved use of the minimal degrees of freedom that are available.

Beyond comparisons of spawning habitat climatology, it may be fruitful to compare actual time series relationships among similar regional ecosystems (a number of recent studies showing environmental/biological relationships for eastern boundary pelagic fishery stocks are cited). Under an assumption of analogy, weak empirical relationships having a similar general form in several systems could be assigned greater confidence than otherwise warranted. Conversely, a high correlation found in one system might be questioned if no suggestion of a similar linkage were found in other systems appearing to be analogous. Arraying identically formulated empirical models from different regional systems might yield patterns among model parameters that could provide insights for predicting effects of human actions or natural perturbations on a given system from the record of previous similar events in other systems.

RESUMEN

Los intentos empíricos de relacionar las variaciones en el reclutamiento con variaciones ambientales o en las comunidades biológicas no han sido demasiado exitosos. Ello se debe, en parte, a las series demasiado breves de datos que generalmente se dispone para los análisis empíricos. Es obvio que debemos desarrollar generalizaciones para proveer una base con el fin de unificar los fragmentos de experiencia disponibles en un marco de trabajo coherente.

Los ecosistemas de las cuatro principales regiones de corrientes de margen oriental, *i.e.*, California, Perú, Canarias, y Benguela, parecen estar controlados por esquemas dinámicos semejantes (se presentan las distribuciones primaveral tardía características de anomalías térmicas costeras y transporte de Ekman en los cuatro sistemas regionales, complementando la información previa acerca de las distribuciones invernal y estival). Estas regiones contienen conjuntos de peces explotables muy semejantes e historias similares en lo que se refiere al crecimiento y abrupta declinación de las pesquerías. Estas semejanzas sugieren que las comunidades de peces en estos sistemas diferentes pueden funcionar de manera semejante con respecto a sus ambientes, y pueden tener estrategias reproductivas para problemas ambientales similares. Dado que la selección natural implica que las estrategias reproductivas consistan en respuestas a los factores más importantes que regulan el éxito reproductivo, los obligatoriamente análogos modelos de hábitos reproductivos y de características ambientales pueden reflejar mecanismos causales importantes. Estos hallazgos, que son independientes de los resultados de las series temporales, proveen una guía para seleccionar variables para modelos de series de tiempo de manera tal que se optimiza el aprovechamiento de la cantidad mínima de grados de libertad disponibles.

Mas allá de la comparación de la climatología de los habitat de desove, puede resultar provechoso comparar las relaciones entre series de tiempo reales entre ecosistemas regionales similares (se mencionan varios estudios recientes que muestran las relaciones ambientales/biológicas en stocks pesqueros pelágicos en áreas de margen oriental). Asumiendo la analogía, podría asignarse mayor confianza a las relaciones empíricas débiles que poseen un formato general semejante en varios sistemas. Recíprocamente, una alta correlación en un sistema podría ser cuestionada si no se encuentra evidencia de una vinculación semejante en otros sistemas que parecen ser análogos al primero. El ordenamiento de modelos empíricos de formulación idéntica provenientes de sistemas regionales diferentes puede brindar patrones entre los parámetros de los models; estos patrones podrían suministrar información útil para predecir los efectos del accionar humano o de las perturbaciones naturales sobre un sistema dado, sobre la base del registro de eventos anteriores semejantes.

INTRODUCTION

The recruitment problem, which has been called the central problem of fish population dynamics (Beyer 1981), remains unsolved after decades of scientific interest and effort. The term "recruitment" refers to *the quantity of younger fish surviving the various egg, larval, juvenile, etc., stages to reach a size at which they become susceptible to fishing gear and thus begin to be sampled by the fishery.* The term therefore integrates the entire period during which the populations are invisible to humans, between the formation of reproductive products in the parental fishes and the later remanifestation of these products as progeny of harvestable size. It thus spans a lengthy continuum of susceptibilities to mortality involving a great range of processes by which the thousands of eggs spawned in the lifetime of a given female must, on average, be reduced to approximately two surviving adult fish.

As might be expected from such a tenuous chain of circumstances, recruitment is notoriously variable. In populations of fishes like anchovies, sardines, and mackerels, the ratio between parental stock size and resulting recruitment typically varies from year to year by factors up to several hundred. Such extreme variability, since it cannot be accounted for mechanistically, introduces a very large noise component into fishery population time series, and largely obscures the signals essential for managing human impacts on the biological system. These signals include evidences of stock-recruitment relationships, multispecies interactions, etc.—knowledge of which could govern fishery development and management strategies. Indeed, the need to account for quasi-random, large-amplitude variations in order to reveal essential mechanisms responding to human alterations of marine biological population structures probably presents, in many cases, a stronger argument for scientific efforts on the recruitment question than does the more often cited need for early prediction of a following year's recruitment. In recognition of the need for progress in this area, an International Recruitment Project (IREP) is the primary focus of the major new international program Ocean Science in Relation to Living Resources, cosponsored by the Intergovernmental Oceanographic Commission and the Food and Agriculture Organization of the United Nations (Anon 1985). For CalCOFI, in particular, the recruitment question could be considered the core scientific issue (Marine Research Committee 1950).

There seems to have been a remarkable lack of progress since the importance of the recruitment problem was recognized early in this century. However, when one considers the nearly total lack of direct information about the fairly complex series of events involving nutrition and associated growth or starvation; predation (which is size-dependent and therefore growth-dependent); transport processes (perturbations of which may disrupt well-tuned adaptations for placing large numbers of individuals in proper habitats for required life-cycle transitions); physiological stresses; etc., the problem's resistance to solution is not so surprising (Table 1). In addition, even where some data are obtainable, difficulties in coping with the interference of strong intrinsic annual periodicities has led to a conventional practice of pooling shorter-scale variations into annual composites; this has further exacerbated the difficulties of empirical analysis by (1) lowering the available signal-to-noise ratios in both environmental and biological time series, (2) severely limiting the number of data points available in reasonably stationary time series, and (3) scrambling together different causal mechanisms controlling different shorter-period survival variations within the same annual composite data point.

Because of the wide variety of possible linkages of environmental fluctuations to recruitment variations (Table 1), and because a variety of oceanographic, meteorological, or other proxy time series may be available to somehow be associated with one or more of these linkages, correlations with short available series of annually composited survival estimates can generally be found and readily justified according to some ecological mechanism. When such a correlation happens to be high enough to meet standard significance

TABLE 1
Some Hypothetical Controls on Survival of Early Life Stages of Fishes

I. Starvation hypotheses
- Turbulent mixing of fine-scale food particle strata
- Low productivity of system
- Wrong type of potential food organisms
- Dispersion of food due to divergent flow pattern
- Mismatch with seasonal food succession caused by anomalies in growth rate

II. Predation hypotheses
- Incidence of small planktonic predators
- Incidence of large planktonic predators (coelenterates, etc.)
- Incidence of predatory adult fish
- Incidence of predatory larval fish
- Variations in growth with size-dependent predation

III. Advection hypotheses
- Offshore transport (removal of drifting larvae from favorable habitat)
- Onshore transport (exposure of larvae to damage in surf zone, etc.)
- Disruption of normal current patterns to which reproductive habits are tuned

IV. Physiological stress hypotheses
- T, S, or [O_2] conditions not within physiological range
- Effects of environmental pollution

V. Disease hypotheses
- Infectious outbreaks, etc.

criteria, it becomes publishable as an advance in scientific understanding, whereas slightly weaker correlations do not. This happens even though, given the complexity of the ecological systems involved, it may be quite unreasonable to expect such overwhelming control of survival by any single environmental variable or process as to yield significant (e.g., $P < 0.05$, etc.) nonspurious correlations from the very short data series typically available, particularly since the real degrees of freedom in both environmental or biological time series are often substantially fewer than the number of annual data points because of interyear serial correlation.

Thus, we have the situation that most of the published empirical environment/recruitment relationships are probably (at least to some degree) spurious, with others that may have represented realistic levels of linkage having been discarded as nonsignificant. Tacit recognition of this situation by the fisheries science community has led to a general low opinion of such relationships, with the result that they are not often used in serious decision-making procedures and thus presently are of little practical value.

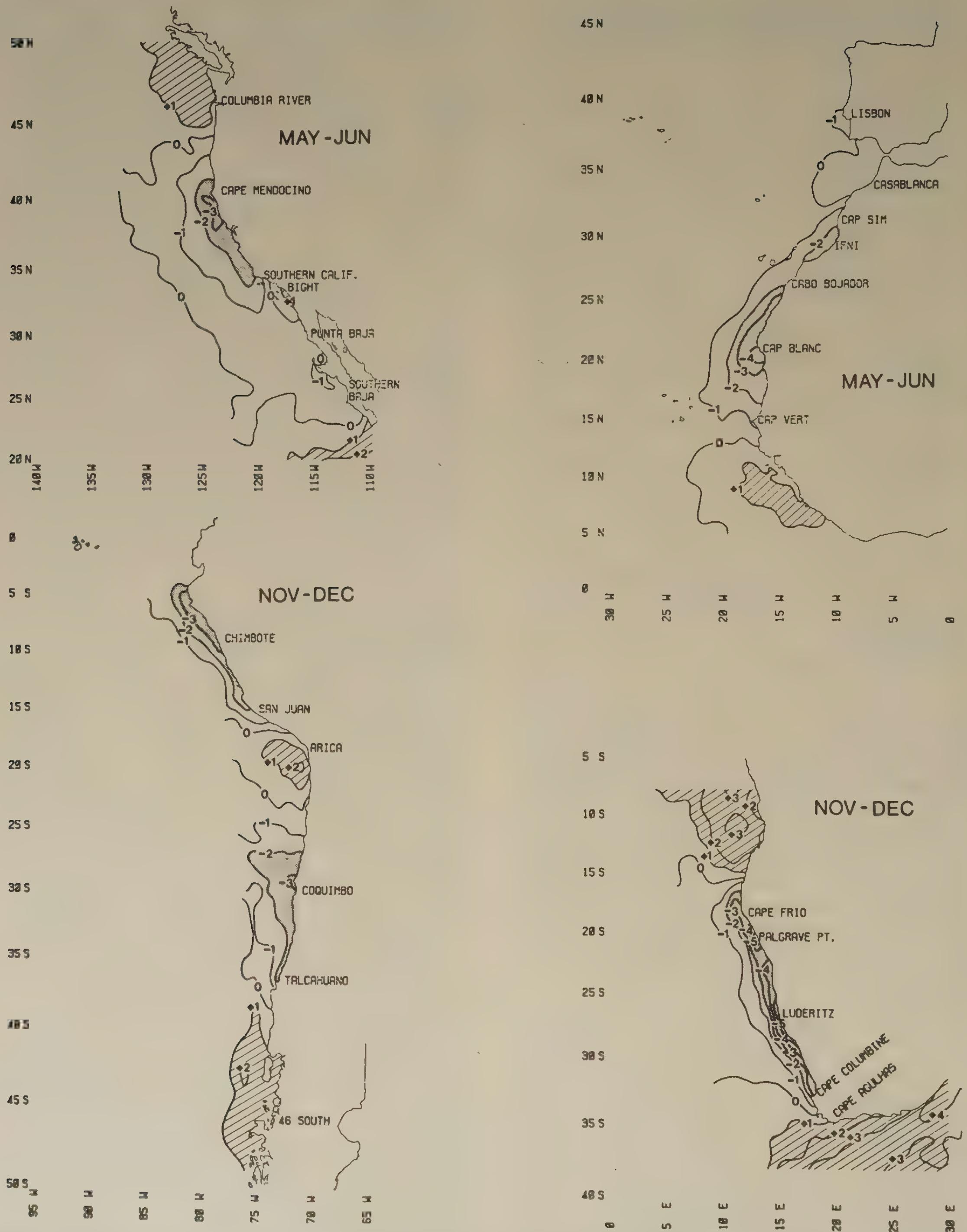
The following sections of this paper attempt to illustrate a rationale for interregional comparative studies directed toward (1) providing a framework for systematizing fragmentary information and insights in order to foster useful generalities concerning physical, biological, and (most important for management activities) human impacts on recruitment, and (2) developing a basis for detecting spurious relationships and for increasing confidence in certain weak relationships by comparisons with similar situations in other regional ecosystems. Objections regarding the possibility of discrediting certain valid relationships in situations where the assumption of analogy may be faulty can be answered with the observation that such relationships are essentially useless anyway in a situation where the valid cannot be distinguished from the spurious.

The comparative method and the experimental method are the two great methods of science (Mayr 1982). The comparative method is particularly indicated in situations not amenable to controlled experiments, and it has underlain nearly all the revolutionary advances in evolutionary biology, to cite one example. It seems surprising that the method has not found wider use in the fishery-environmental field, which appears to have been preoccupied with diversity rather than synthesis, and prone to view each local situation as unique.

COMPARATIVE SPAWNING HABITAT CLIMATOLOGY

Parrish et al. (1983) presented maps of two-month (Jan.-Feb. and July-Aug.) long-term mean distributions of various environmental characters for the four major eastern boundary regions of the world: the California, Peru, Canary, and Benguela current systems. These maps generally represented seasonal extremes in each system; however, peak upwelling in the temperate areas is generally earlier toward the equator. The summer and winter maps of Parrish et al. are supplemented here by characteristic late spring (May-June, N. Hemisphere; Nov.-Dec., S. Hemisphere) distributions of coastal temperature anomaly (Figure 1) and Ekman transport (Figure 2).

Negative coastal temperature anomalies greater than 2°C (i.e., 2 degrees cooler than at the same latitude some 1,000 km offshore; stippled in Figure 1) delimit the major upwelling centers. Note the definite separation of the two distinct major upwelling regions off South America. Warm anomalies (areas of positive anomaly greater than 1°C are diagonally hatched in Figure 1), or areas where cold anomalies are less intense, often correspond to spawning regions of coastal pelagic fishes (Parrish et al. 1983). Ekman transport vectors illustrate the strong offshore surface transport that must be accommodated in reproductive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PUNTA BAJA
SOUTHERN BAJA
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CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
+3
+4
-5

Figure 1. Coastal temperature anomaly (difference from characteristic temperature at similar latitude some ten degrees longitude offshore) distributions in the four major eastern boundary current systems, characterizing late spring conditions in the respective hemispheres. Units are degrees Celsius. Corresponding winter and summer maps, and details of their construction, are presented by Parrish et al. (1983).

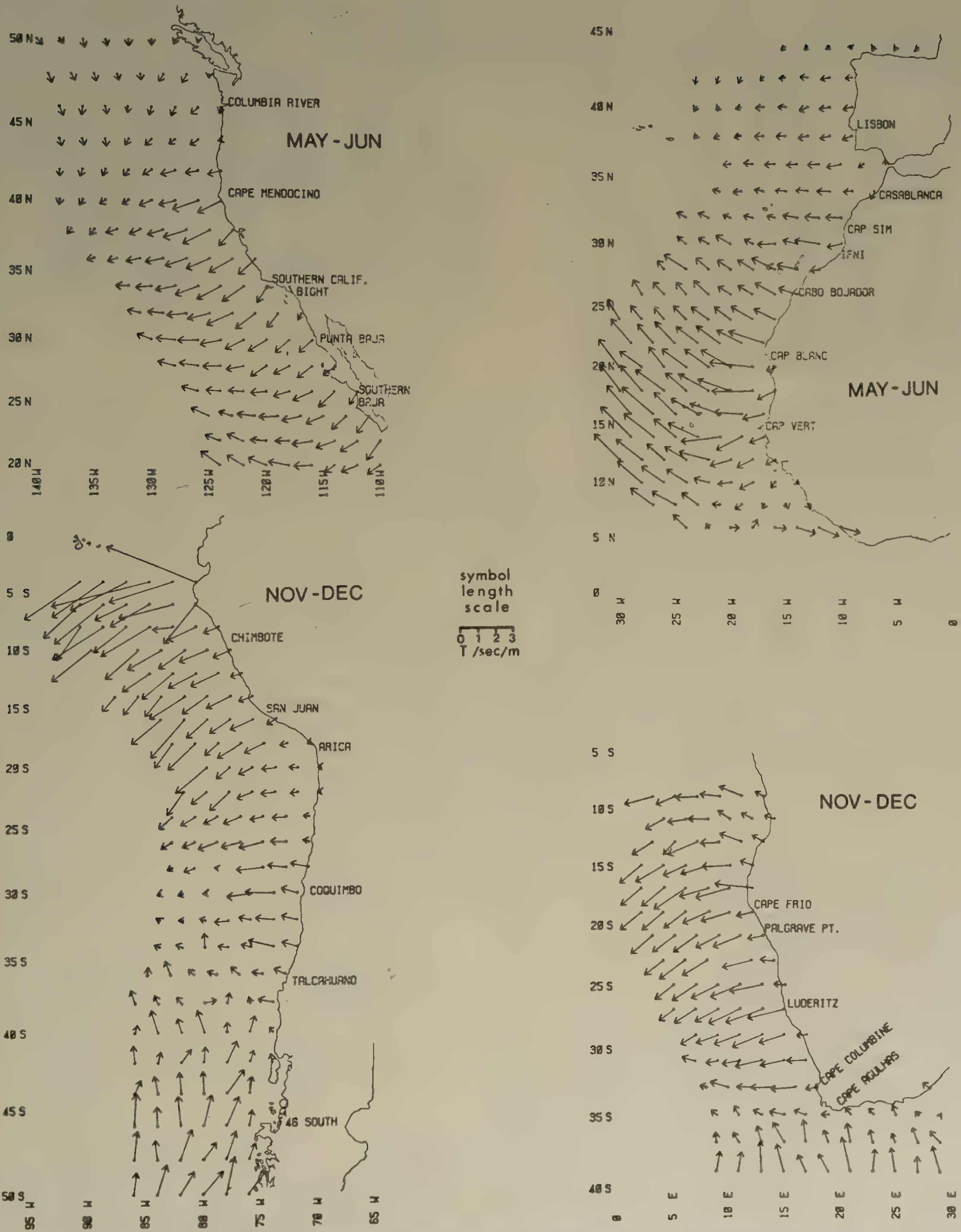
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Figure 2. Surface Ekman transport distributions in the four major eastern boundary current systems, characterizing late spring conditions in the respective hemispheres. Transport is proportional to vector symbol length. A symbol length scale is provided; units are metric tons per second across each horizontal meter width. Corresponding winter and summer maps, and details of their construction, are presented by Parrish et al. (1983).

TABLE 2
Dominant Anchovy, Sardine, Jack (Horse) Mackerel, Hake, Mackerel, and Bonito in the Four Major Eastern Boundary Currents

California Current	Canary Current
Engraulis mordax	*Engraulis encrasicholus*
Sardinops sagax	*Sardina pilchardus*
Trachurus symmetricus	*Trachurus trachurus*
Merluccius productus	*Merluccius merluccius*
Scomber japonicus	*Scomber japonicus*
Sarda chiliensis	*Sarda sarda*
Peru Current	Benguela Current
Engraulis ringens	*Engraulis capensis*
Sardinops sagax	*Sardinops ocellatus*
Trachurus symmetricus	*Trachurus trachurus*
Merluccius merluccius	*Merluccius capensis*
Scomber japonicus	*Scomber japonicus*
Sarda sarda	*Sarda sarda*

After Bakun and Parrish (1980)

strategies of marine organisms inhabiting these regions (Figure 2). In addition, McLain et al. (1985) and Shelton et al. (1985) show that biological communities, not only in the Pacific systems but apparently also in the Atlantic, must cope with intermittent extreme warm episodes of El Niño-type intensity.

Very similar assemblages of dominant coastal pelagic fish species inhabit the four regions (Table 2). In each region there is a dominant anchovy, sardine, jack mackerel, hake, mackerel, and bonito. In several cases, the same nominal species inhabits more than one of the regions. In other cases, the species are so similar that their difference may be more a matter of assumption than of demonstration (R.H. Parrish, pers. comm.). There have also been similar regional experiences of rapid fishery expansions and precipitous declines (Parrish et al. 1983).

The various environmental and biological similarities suggest that fish communities in these different regional systems may function similarly with respect to their environments and may be solving similar problems in their reproductive strategies. Survival of offspring to the age of reproduction, which often approximates the age of fishery recruitment, is the direct causative factor in the selective process. Thus natural selection demands response to the most crucial mechanisms regulating recruitment. This implies that we can use the observed results of natural selection in terms of geographical and seasonal aspects of reproductive strategies to understand the causes controlling reproductive success. In other words, pervasive patterns of reproduction. with respect to environmental characteristics, may indicate the actual environmental mechanisms regulating recruitment success.

For example, Parrish et al. (1983) found a general pattern in the spawning habits of anchovies and sardines that seemed to point to a simultaneous minimization of both wind-induced turbulent mixing and offshore-directed transport. Thus the starvation hypothesis, as expressed in Lasker's (1981) scenario of turbulent dispersion of fine-scale food strata, and the transport hypothesis, involving detrimental transport of larvae away from favorable proximity to the coast, are implicated as important mechanisms to be considered in modeling and exploratory data analysis. Temperature of spawning showed much less coherent pattern, suggesting that selection of spawning habitat for any particular optimum temperature is less important than minimizing turbulent mixing or offshore transport.

Certain initially puzzling discrepancies from the general patterns have proved enlightening. For example, Bakun and Parrish (1982) reported that the Peruvian anchoveta, by far the largest fish stock on record before its collapse, stood out as an anomaly in that its spawning peak during austral winter occurred at the very season when offshore Ekman transport was most intense (Figure 3; Table 3), rather than when it was relatively weak, as is the general pattern. However, when mixed layer depth climatologies were produced for the various regions (Parrish et al. 1983), the discrepancy was apparently resolved. Seasonal variation of mixed layer depth off Peru proceeds in phase with that of transport but has greater amplitude (Figure 4), with the result that the thinner mixed layer of austral summer is apparently carried offshore some four times as fast as is the deeper winter mixed layer (Figure 5), even though the winter transport (by volume) is nearly twice as large. Thus the spawning season does indeed appear to be tuned to minimize the rate of offshore loss of eggs and larvae within the ocean's upper mixed layer. This resolution of what initially seemed a discrepancy of a single situation from the general pattern has thus pointed out the generality that, in treating the mechanism of offshore loss of reproductive products distributed in the mixed layer, estimates of wind-driven surface (Ekman) transport should ideally be divided by the effective mixed layer depth to yield an *Ekman velocity of the mixed layer*[1]. In this way we are able to combine two environmental variables to yield a

---

[1] In the statement that these two variables should ideally be combined, the qualification "ideally" is important. Ekman transport is estimated from relatively abundant surface wind reports, which reflect the fairly large spatial scales of atmospheric variation. Mixed layer depth varies on much shorter oceanic length scales and must be determined from more sparsely distributed subsurface measurements. Thus there may be cases where the effective mixed layer depth is so imprecisely determined that the combined variable yields a less reliable indicator of interyear variation of offshore velocity than would be provided by the interyear variation in the Ekman transport estimate itself.

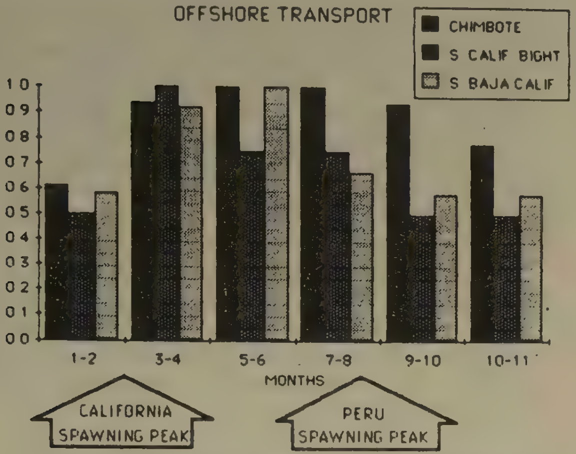

Figure 3. Offshore-directed Ekman transport within the spawning grounds of the Peruvian anchoveta (Chimbote) and within the spawning grounds of the central and southern subpopulations of (California Current) northern anchovy, by 2-month segments of the annual cycle. Units are scaled relative to the seasonal maximum in each area, which is assigned the value 1.0 in all three locations in order to scale them similarly (and thereby to emphasize seasonal timing rather than absolute magnitude). Timing of seasonal peak spawning in the two systems is indicated by the wide arrows. (See Table 3 for unscaled numerical values.)

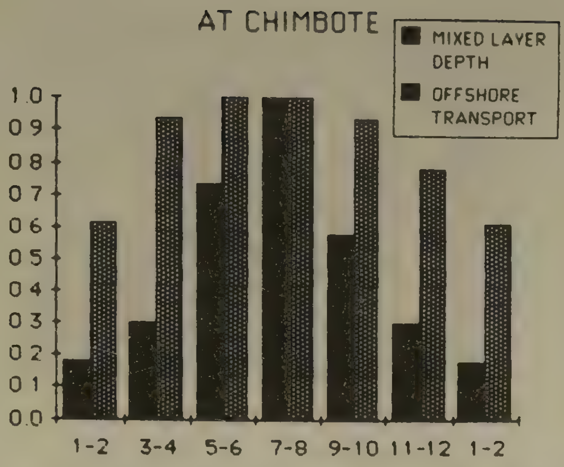

Figure 4. Offshore-directed Ekman transport and mixed layer depth within the spawning grounds of the Peruvian anchoveta, by 2-month segments of the annual cycle. Units are scaled relative to the respective seasonal maxima, which are assigned the value 1.0 in both cases in order to place both on a common scale (and to thereby emphasize seasonal timing rather than absolute magnitude). (See Table 3 for unscaled numerical values).

single more meaningful variable, thereby conserving degrees of freedom for improving the power of hypothesis tests.

The major point to be made is that such findings, which are based on patterns in the long-term composite averages, are independent of any results based on examination of the available time series data. Thus the findings provide a guide to selecting variables for time series analysis so that the selection process itself does not deplete the scarce degrees of freedom. One could say that the observed characteristic seasonality and geography of reproductive strategies results from a large number of "trial-and-error experiments" performed by the population over the period of development. Moreover, natural selection ensures that this observed result is the "most correct" one for the fish, at least in the long term (providing that we are observing truly long-term adaptations).

TABLE 3

Actual (Unscaled) Values Used to Construct Figures 3, 4, and 5

Transport ($T\ sec^{-1}\ m^{-1}$)

Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	1.1	1.7	1.8	1.8	1.7	1.4
S. Calif. Bight	0.2	0.4	0.3	0.3	0.2	0.2
S. Baja Calif.	0.7	1.1	1.2	0.8	0.7	0.7

Mixed Layer Depth (m)

Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	7	12	29	40	23	12
S. Calif. Bight	37	25	11	10	14	20
S. Baja Calif.	45	23	18	9	20	34

Net Offshore Velocity of Mixed Layer ($km\ day^{-1}$)

Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	13.6	12.2	5.4	3.9	6.4	10.1
S. Calif. Bight	0.5	1.4	2.4	2.6	1.2	0.9
S. Baja Calif.	1.3	4.1	5.8	7.7	3.0	1.8

Transport and mixed layer depth climatologies taken from Parrish et al. (1983); offshore velocities computed as the quotient of the two.

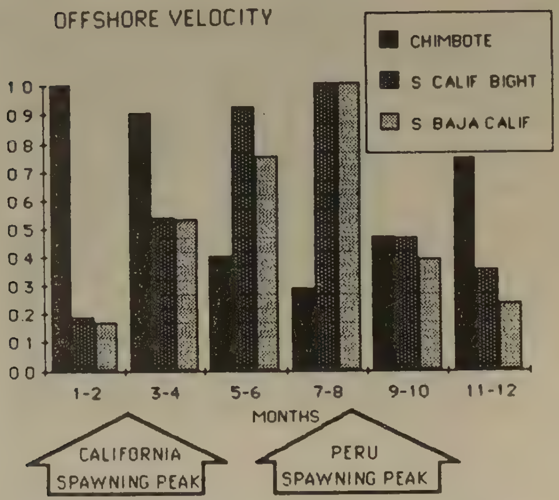

Figure 5. Offshore-directed velocity of the surface mixed layer (Ekman transport divided by mixed layer depth) within the spawning grounds of the Peruvian anchoveta (Chimbote) and of the central and southern subpopulations of (California Current) northern anchovy, by 2-month segments of the annual cycle. Units are scaled relative to the seasonal maximum in each area, which is assigned the value 1.0 in all three locations in order to scale them similarly (and thereby to emphasize seasonal timing rather than absolute magnitude). Timing of seasonal peak spawining in the two systems is indicated by the wide arrows. (See Table 3 for unscaled numerical values.)

Thus any empirical relationship based on short time series of recent data on reproductive success and on variations in some environmental characteristic, not corroborated by any apparent reproductive accommodation to that characteristic, might be of questionable validity. Conversely, an empirical relationship reflected in what seems to be an obvious adaptation in characteristic reproductive habits could be assigned increased confidence. This line of reasoning seems applicable even to a unique situation where no assumed analogues are available for comparison, but the comparative aspect introduces a more powerful test. For example, an apparent adaptation may be mere happenstance in a single situation. However, given the regional diversity introduced by varying coastline orientations, atmospheric regimes, advected characteristics, etc., it is unlikely that strong interregional correspondence of reproductive habits with environmental characteristics is due merely to happenstance. Therefore, recognition of such an interregional pattern provides much stronger confirmation of real mechanistic linkage. And, as noted in the Introduction, the present need in recruitment research is for any substantial error to be on the side of undue conservatism and rigor, if results are to be applicable to real problems.

At Pacific Environmental Group we are presently entertaining the notion that the coastal pelagic fishes of the more tropical eastern boundary areas (the sardinellas, etc.) may be playing the same basic survival "game" as those (sardines, anchovies, etc.) in the temperate zones, but at a warmer temperature range. If this is even partially true, the Angola, Guinea, and Costa Rica Dome coastal regions, the Ivory Coast-Ghana upwelling region, the Malabar Coast of India, etc., would provide another set of spawning habitat seasonalities and geographies with which to sharpen these interpretations. Other possibilities for instructive analogues include such western ocean boundary stocks as the Brazilian sardinella and the Japanese sardine; in these cases, basic differences in the environmental dynamics of the systems should be carefully evaluated.

COMPARATIVE TIME SERIES MODELING

Beyond comparisons of long-term mean characteristics of spawning habitats and biological consequences, it may be fruitful to compare empirical (time series) models among similar regional systems. There have been a number of published suggestions of environmental/biological relationships. (Some of the more recent examples for eastern boundary coastal pelagic fishery stocks are cited in Table 4.) Formulations and points of view have differed greatly among researchers concerned with the different regional systems. For example, I believe that Boyd's (1979) formulation in terms of sea-temperature variance, the results of which suggest Lasker's (1981) mechanism of turbulent dispersion of fine-scale food concentrations, has not been tried in the California Current or the other systems.

Systematic comparisons of identical empirical model formulations for all available "analogous" situations might yield suggestive patterns among model parameters to provide new insights into the processes controlling the biological systems. The comparisons could also yield information about the validity of attempts to transfer "experience" among systems (e.g., predicting consequences of human actions or natural perturbations in one system from the record of similar events in other systems, etc.). Under an assumption of analogy, empirical relationships having a similar general form in more than one system might be correctly afforded greater interest and confidence than otherwise warranted. Conversely, a correlation found in one system might be considered questionable if no suggestion of similar linkage were found in other systems appearing, in other respects, to function analogously.

For example, consider the following set of formulations (the variables illustrated in this example are perhaps most suitable to anchovies)

$$
\begin{aligned}
\log (R_i/S_i) &= a_{1,i} + B_{1,i} S_i^c \qquad 0 \leq c \leq 1 \\
\log (R_i/S_i) &= a_{2,i} + B_{2,i} u_i \\
\log (R_i/S_i) &= a_{3,i} + B_{3,i} \bar{u}_i \\
\log (R_i/S_i) &= a_{4,i} + B_{4,i} W_i \\
\log (R_i/S_i) &= a_{5,i} + B_{5,i} T_i \\
\log (R_i/S_i) &= a_{6,i} + B_{6,i} \tau_i \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
\log (R_i/S_i) &= a_{m,i} + B_{j,i} S_i^c + B_{k,i} u_i \\
\log (R_i/S_i) &= a_{m+1,i} + B_{j+1,i} S_i^c + B_{k+1,i} u_i \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
\log (R_i/S_i) &= a_{p,i} + B_{q,i} S_i^c + B_{r,i} u_i + B_{s,i} \bar{u} \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
&\cdots\cdots\cdots\cdots\cdots\cdots \\
&\cdots\cdots\cdots\cdots\cdots \text{ etc.}
\end{aligned}
$$

where R_i is recruitment to a given fish stock "i",
S_i is adult stock size,
u_i is upwelling index coincident in time and space with spawning (we might generally expect strong upwelling to be a detrimental factor, involving loss of eggs and larvae via offshore transport),
$\bar{u}_i$ is a properly space- and time-lagged upwelling index that would reflect longer time-scale nutrient inputs to the system at upstream upwelling centers,
W_i is wind-generated turbulence input to the larval habitat (motivation for the choice of variables u_i, $\bar{u}_i$, and w_i can be found in Bakun and Parrish 1980),
T_i is an index of characteristic temperature,
τ_i is temperature variance as used by Boyd (1979), etc.

The dots indicate that other hypothesized factors and combinations of factors would also be considered.

The log (R/S) formulation simply connotes a multiplicative effect of the explanatory vari-

TABLE 4

Examples of Recent Studies Indicating Environmental/Biological Relationships for Eastern Boundary Current Pelagic Fishery Stocks

California Current

Lasker (1981)—northern **anchovy** (*Engraulis mordax*)—negative effect of wind-generated turbulence (wind cubed index) during spawning season.

Parrish and MacCall (1978)—Pacific **mackerel** (*Scomber japonicus*)—positive effect of upwelling (index) at spawning ground previous to spawning (one-month lag).

Bakun and Parrish (1980)—Pacific **sardine** (*Sardinops sagax*)—positive effect of upwelling (index) in upwelling maximum region upstream of spawning grounds (800-km spatial lag) integrated over previous calendar year (2- to 14-month spatial lag).

Bailey (1981)—Pacific **hake** (*Merluccius productus*)—negative effect of offshore transport (upwelling index) during planktonic larval period.

Collins and MacCall (1977)—Pacific **bonito** (*Sarda chiliensis*)—positive effect of upwelling (index) during spawning season.

Peru Current

Various authors—**anchoveta** (*Engraulis ringens*)—negative effect of El Niño (often attributed to lowered primary productivity).

Benguela Current

Boyd (1979)—Southwest African **anchovy** (*Engraulis capensis*)—negative effect of sea-surface temperature variance during spawning season.

Canary Current

Belveze and Erzini (1983)—**sardine** (Moroccan central zone; *Sardina pilchardus*)—positive relation of catches to upwelling (index) averaged over the three previous spawning seasons (catch is composed of one- two-, and three-year-olds).—**mixed small pelagics** (Moroccan northern zone; mostly *S. pilchardus*)—high catches in low-rainfall years.

Freón (1983)—**sardinella** (Senegal)—positive relation of CPUE to wind speed during upwelling season (previous winter); author suggests autocorrelation in wind series as explaining a recruitment effect.

Guinea Current

Bakun (1978)—Ghanain herring (**Sardinella** *aurita*)—negative relation of catch to rainfall and sea-surface temperature (related to upwelling).

Binet (1982)—**sardinella** (Ivory Coast and Ghana; *S. maderensis* and *S. aurita*)—positive effect of upwelling (temperature index) and negative effect of coastal runoff on catch.

Cury and Roy*—**sardinella** (Ivory Coast and Ghana; *S maderensis* and *S. aurita*)—positive effect on catch and on reproductive success of local upwelling (temperature index), which is related to remote forcing by wind stress variations in the western equatorial Atlantic (i.e., off Brazil).

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*Cury, P., and C. Roy. MS. Modelisation de l'abondance des especes pelagiques cotieres de Cote d'Ivoire integrant l'effort de peche et un indice d'upwelling ORSTOM, 24 Rue Bayard, 75008 Paris, France.

> ables; i.e., if an increase of a given variable were to double predicted survival per unit spawning biomass, then an equal decrease would halve predicted survival rather than reduce it to zero, as would be required by an additive (i.e., nonlogarithmic) formulation. The exponent c represents MacCall's (1980) suggestion for the incorporation of variable habitat dimension in a density-dependent mechanism such as adult cannibalism (where if $c = 1$, there is no habitat size variation and the result is a normal Ricker curve; if $c = 0$, the habitat size is proportional to stock size and therefore density does not increase with abundance, so that there is no stock-size dependence through the density-dependent mechanism; $0<c<1$ implies the less-than-proportional increase of habitat volume with stock size, which fits observation).

The set of formulations would then be fitted to the available data for various "analogous" stocks in similar environmental settings. Thus we fit univariate regressions, and then various multiple regression combinations of the selected explanatory variables, for each stock and spawning habitat. Then we array the total set of model parameters for the various stocks and look for informative patterns.

Obviously, among a large number of models like this, a certain number of fits satisfying significance criteria will always appear, if only by chance correspondence of unrelated variations. For example, if one does not find at least one fit at the $P = 0.05$ significance level out of twenty attempts, one is simply unlucky. But even if each researcher were limited scrupulously to a prior choice of a single formulation, it would not necessarily improve the utility of published results; we have no idea of how many unpublished failures to meet significance criteria may have occurred for each publishable success. In fact, given the multitude of possible interactions with growth, predation, transport processes, physiological stress, etc., at various life stages, it seems almost inconceivable that any one mechanism could so dominate total survival as to yield a strong univariate relationship that was not to some degree spurious. Thus, searching for "significant" empirical relationships may be an exercise in self-delusion. If the weaker relationships that may represent realistic levels of control by particular mechanistic linkages are to be usable, ways must be found to cull out the larger number of spurious chance fits resulting from relaxed significance criteria. If one finds patterns of similar form among relationships, similar signs of model parameters, etc., for analogous situations, even though the relationships are too weak individually to meet ordinary significance criteria, valuable insight may have been gained. If nothing is found but chaos suggesting unrelated random combinations, one might conclude that little confidence should be placed in any such models based on the really inadequate degrees of freedom represented by short autocorrelated recruitment time series.

CONCLUDING REMARKS

This paper is intended to serve as the convener's introduction to the invited papers for the Symposium on Comparative Studies of Eastern Ocean Boundary Systems at the 1984 CalCOFI Conference. Certain of these introductory remarks may seem negative; their purpose is to indicate that at this stage in the development of fisheries/environmental science, the likelihood that there is no such thing as an exact analogy among large marine ecosystems does not rule out interregional comparison as a useful deductive tool. In using interregional comparison as a gauge for validity of findings, inconsistency with an interregional pattern is of course no proof of spuriousness; however, interregional consistency may provide otherwise unavailable support for a statistically weak but potentially useful result.

In view of the great resources required for experiments covering the range of time and space in recruitment variability of a fish stock, the cost-effectiveness of the comparative approach deserves mention. In many cases the observational investment will already have been made. Maritime reports (such as those used in the construction of all the figures in this paper) are available, at varying density, for all the oceans of the world. Some fishery research studies will have been made in any area containing a substantial exploited fish stock. Thus the costs of a rudimentary comparative study may be little more than those involved in acquiring existing data and arraying them in similar formats.

Fishery/environmental science clearly needs generalities and unifying principles with broad applicability. Consider, for example, the situation at the FAO Technical Consultation to Examine Changes in Abundance and Species Composition of Neritic Resources (held in Costa Rica in 1983) where, at a major gathering of fishery scientists from all over the world, no consensus could be found (e.g., Bakun 1983) as to the probable consequences of continuing to take record sardine catches off northern Chile in the presence of the 1982-83 El Niño, even then recognized as the strongest environmental anomaly in the eastern Pacific for at least fifty years. We certainly expect that valid generalities do exist in the fishery/environmental field, as in other branches of science. Identifying them and making them available for fishery management and industrial decision making should be given high priority.

The following symposium papers present selected comparative aspects of the four major eastern ocean boundary ecosystems of the world and their associated fisheries. No attempt has been made to assemble a comprehensive and coherent comparative treatment. Our purpose is to provide some examples of ongoing comparative research, some useful insights into the degree of analogy presented by these four similar systems, and some basic information to aid comparative interpretation and deduction. Most important, we hope to stimulate fisheries scientists to maintain a comparative focus in their research efforts.

LITERATURE CITED

Anonymous. 1985. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, Reports of meetings of experts and equivalent bodies SC-85/WS/18. Intergovernmental Oceanographic Commission, Unesco, Paris, 35 p.

Bailey, K.M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. Ser. 6:1-9.

Bakun, A. 1978. Guinea Current upwelling. Nature 271:147-150.

———. 1983. Part III—Report of the working group on environmental studies and monitoring. *In* G.D. Sharp and J. Csirke (eds.), Reports of the expert consultation to examine changes in abundance and species composition of neritic fish resources, San José, Costa Rica, April 1983. FAO Fish. Rep. 291(1):41-54.

Bakun, A., and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions. *In* G.D. Sharp (ed.), Workshop on the effects of environmental variation on the survival of larval pelagic fishes, Lima, Peru, April-May, 1980. IOC Workshop Rep. 28, Unesco, Paris, p. 67-104.

———. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep. 23:99-112.

Belveze, H., and K. Erzini. 1983. The influence of hydroclimatic factors of the availability of the sardine (*Sardina pilchardus* Walbaum) in the Moroccan Atlantic fishery. *In* G.D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, San José, Costa Rica, April 1973. FAO Fish. Rep. 291(2):285-327.

Beyer, J.E. 1981. Aquatic ecosystems—an operational research approach. Univ. Wash. Press, Seattle, 315 p.

Binet, D. 1983. Influence des variations climatiques sur la pêcherie des *Sardinella aurita* ivoiro-ghanéennes: relation sécheresse-surpeche. Oceanologica Acta 5(4):443-452.

Boyd, A.J. 1979. A relationship between sea surface temperature variability and anchovy *Engraulis capensis* recruitment of Southwest Africa, 1970-1978. Fish. Bull. S. Afr. 12:80-84.

Collins, R.A., and A.D. MacCall. 1977. The California Pacific Bonito resource, its status and management. Calif. Dept. Fish Game, Mar. Res. Tech. Rep. 35, 39 p.

Fréon, P. 1983. Production models as applied to sub-stocks depending on upwelling fluctuations. *In* G.D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, San José, Costa Rica, April 1983. FAO Fish. Rep. 291(3):1047-1064.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. *In* R. Lasker and K. Sherman (eds.), The early life history of fish: recent studies. The Second ICES Symposium, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 178:375-378.

MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. *In* G.D. Sharp (ed.), Workshop on the effects of environmental variation on the survival of larval pelagic fishes, Lima, Peru, April-May, 1980. IOC Workshop Rep. 28, Unesco, Paris, p. 201-220.

Marine Research Committee. 1950. California Cooperative Sardine Research Program progress report 1950. California State Printing Office, 54 p.

Mayr, E. 1982. The growth of biological thought. Harvard Univ. Press, Cambridge, Mass., 974 p.

McLain, D.R., R. Brainard, and J. Norton. 1985. Anomalous warm events in eastern boundary current systems. CalCOFI Rep. 26:(this volume).

Parrish, R.H., and A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dept. Fish Game, Fish. Bull. 167, 109 p.

Parrish, R.H., A. Bakun, D.M. Husby, C.S. Nelson. 1983. Comparative climatology of selected environmental factors in relation to eastern boundary pelagic fish reproduction. *In* G.D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, San José, Costa Rica, April 1983. FAO Fish. Rep. 291(3):731-777.

Shelton, P.A., A.J. Boyd, and M.J. Armstrong. 1985. The influence of large-scale environmental processes on neritic fish populations in the Benguela Current system. CalCOFI Rep. 26:(this volume).

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History of Sea Turtles at Polihua Beach on Northern Lanai

by George H. Balazs

The only site in the main Hawaiian Islands with a well-documented history of nesting sea turtles is Polihua, a mile-long white sand beach on the northern shore of Lanai, just east of Kaena Point (Fig. 1). This is also the only location where the traditional Hawaiian place name is descriptive of eggs on a beach (Poli-hua, literally "eggs in bosom," Pukui et al. 1976). The available information suggests that Polihua was an important breeding site for the Hawaiian green turtle, *Chelonia mydas,* until the late 1800's or early 1900's. At present, very little nesting has been reported there or anywhere else in the main Hawaiian Islands. Most of the extant nesting by green turtles in Hawaii takes place at French Frigate Shoals, 300 miles to the northwest of Kauai. Green turtles seasonally migrate to this small isolated site from resident coastal foraging pastures throughout the Hawaiian Archipelago (Balazs 1980). Before 1786, French Frigate Shoals appears to have been unknown, and therefore unexploited, by the people of Hawaii. The area is currently protected as a National Wildlife Refuge. The hawksbill, *Eretmochelys imbricata,* is a second species of sea turtle that nests in the Hawaiian Islands, but solely in the main islands, in small numbers, on a few black sand beaches (Balazs 1978).

There are no reports summarizing the existing knowledge about Polihua and sea turtles, although the significance of the beach has been pointed out in recent publications (Balazs 1975, 1980). In view of the protected status of sea turtles under the U.S. Endangered Species Act, a synthesis of historical information about Polihua and the adjacent coastline of northern Lanai may be helpful to the recovery of the Hawaiian stock. For example, Polihua could prove to be one of the best places in Hawaii to do experimental restocking of green turtles aimed at reestablishing a nesting colony.

Hawaiian Folklore

Hawaiian folklore relates that Polihua played a key role in the arrival of sea turtles to Hawaiian waters. Beckwith (1970) tells the legend of Aiai, the fish demigod, "marking" a stone at Kaena, the northwestern point of Lanai. This stone then turned into the first Hawaiian sea turtle, thereby explaining why turtles come to nearby Polihua to lay their eggs (see also Pukui et al. 1976). Tabrah (1976) lists part of an ancient Hawaiian chant as "Ua ono o Pele i kana i'ia o ka honu o Polihua," which is translated as "Delighted, the Fire Goddess (Pele) feasts on flesh of turtles from Egg-nest Cape." The lines of this chant are said to "... celebrate the fame of the turtles who lay their eggs at that point of the coast called Polihua" (see also Emerson 1915; Fornander 1919-1920; Emory 1924). A traditional hula based on this ancient chant has recently been composed by Elaine Kaopuiki, a native resident of Lanai.

Pukui (1983) records the Hawaiian proverb "Na honu ne'e o Polihua," translated as "The moving turtles of Polihua."

Archaeology

Emory (1924) describes two archaeological sites on the east side of Polihua Valley that are believed to be fishermen's shrines (koa). Except for their proximity to the beach and ocean, no direct evidence was given to relate either of these stone structures to sea turtles. At Kaena-iki, just south of Kaena, Emory (1924) lists a religious stone platform (heiau) said to be one of the largest of its kind on Lanai. Emory (1924) was unable to determine a name for the heiau, since no one had lived in this region of the island for many years.

Exploitation

A series of Hawaiian newspaper articles by Kahaulelio (1902), later translated into English by Mary K. Pukui, contain information about Polihua from the mid-to late-1800's, following abolition of the Hawaiian "kapu system." The relevant sections of the Kahaulelio (1902) account are as follows:

> "Polihua at Lanai was a very famous place for turtle catching. The natives catch them on the sand shore if they need meat. Strangers do too, when they want to visit and see for themselves and if they wanted some to eat. It was a good thing to see this famous fish of the birthplace of my beloved mother who has preceded us yonder when your writer was but a wee child. This was the fish that Pahulu asked the gods not to allow it to have any irritation in its flipper or tail. ... Yes, when you get to Polihua to catch turtles, you need all your strength. It is done thus—go to

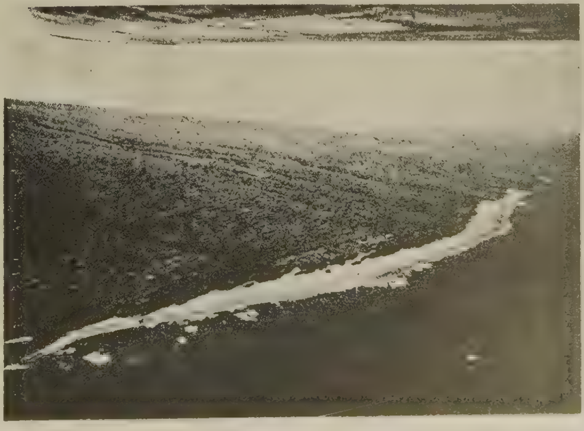

Figure 1. Aerial view of Polihua taken in July of 1977.
Photo by G.H. Balazs

> Polihua in the evening and sleep there and in the early morning, in the twilight, draw close to the edge of the clumps of grass adjoining the sands and there you will see large female turtles returning to the sea. Run as fast as you can to reach a turtle and turn the turtle over with your hands with all your might. If you succeed in turning it over, you are going to eat some turtle meat but if you fail, you'll find yourself in the sea. Your writer has been accustomed as he went to sea frequently to seeing turtles gathered close to the reef. At the time that you see the turtles coming up to breathe, paddle softly until you are very close. The turtle will dive downward and then you'll distinguish it clearly. Dive down and catch it, turn it over as quickly as possible and it becomes very light and easy to land on the canoe. This seems to be the method used by most of the people who relish the greenish luau meat in a turtle. Still the easiest way to catch a turtle is by spearing it and if one speared them at Polihua one caught several times four of them."

Species Confirmation

A description of turtles at Polihua is also given in Gay (1965) for the early 1900's. Gay (1965) states: "Polihua is located near Kaena Point on the northwest coast of Lanai. It was there that the turtles laid their eggs in the sand above the high-water mark. I have seen turtles that weighed in excess of five hundred pounds on this beach and were capable of carrying three medium-sized persons."

It is important to confirm that the species nesting at Polihua was the green turtle, since this is not clearly stated in the historical literature cited above. Evidence for the green turtle includes the chant quoted by Tabrah (1976) and proverb by Pukui (1983) referring to "honu", the green turtle, as opposed to "honu'ea", the hawksbill (Pukui and Elbert 1971). In addition, Kahaulelio (1902) and Gay (1965) mentioned the large size of the turtles at Polihua. This description is consistent with the known size of the adult green turtle, but not the smaller adult hawksbill. Kalaulelio (1902) also said that the turtles at Polihua were captured for food, a practice not usually carried out in Hawaii with the hawksbill since this species was considered poisonous (Malo 1951).

Current Information

Since 1972, I have been able to gather various unpublished material about Polihua through personal correspondence and interviews with several longtime residents of Lanai. The names of these informants are kept anonymous herein to help insure a continuing flow of information, and also because some aspects may be culturally sensitive. The individuals involved include native Hawaiians, as well as other reliable members of the Lanai community. The following information comes from these sources.

The stone image of a "turtle god" is reported to be at Polihua. At one time, the exact location was known by at least one elderly person, but windblown sand has apparently covered up the stone. Efforts have been made to locate the stone in recent years since shifting sand may periodically expose it. The success of these efforts is unknown. There are also reports of a turtle petroglyph located at Polihua, on or near a rocky point at the east end of the beach. Sand was also reported to shift back and forth over this site. It is possible that the stone "turtle god" and the turtle petroglyph are, in fact, one and the same. However, stone "fish gods" (kuula) in the Hawaiian culture usually consisted of a smooth upright movable stone. In contrast, petroglyphs were mostly inscribed on large boulders or other stationary rock. Two of the best known Hawaiian petroglyphs depicting sea turtles appear on a boulder at Luahiwa in the interior of Lanai (Emory 1924).

Two persons recalled from memory the catching of turtles on Polihua Beach during the 1920's. The sharp decline in nesting during subsequent years has been attributed to the construction of roads, increases in traffic to the north shore, and easier access for taking turtles on the beach. A dirt road now leads directly to Polihua. Other possible adverse factors to nesting, which have also been speculated upon, include changes in coastal vegetation and heavy erosion at higher elevations (Balazs 1975).

Adult female Hawaiian green turtle.

Photo by G.H. Balazs

Known or attempted nesting during recent years are listed below. It is possible that some of these reports involve turtles hauled out to bask, rather than to nest. Terrestrial basking is common in the Northwestern Hawaiian Islands, especially at French Frigate Shoals, but rare in the main islands of Hawaii and most other areas of the world (Whittow and Balazs 1982). It should also be noted that several unpublished sightings exist for the Hawaiian monk seal, *Monachus schauinslandi,* both ashore and in the coastal waters of northern Lanai.

- —In 1954, a "turtle eggs nest" was reportedly seen at Polihua "behind a large sand dune near a keawe tree."
- —In 1968, a turtle was seen "up on a north shore beach."
- —In 1971, a turtle was seen right at the water's edge at Polihua.
- —On November 23, 1977 at 1000 h, two large green turtles were seen mating in the sea off Laehi, on the northeastern shore of Lanai.
- —On July 31, 1981 at 1300 h, two "very large turtles" were seen at Polihua "20-30 yards up the beach" near some boulders. No eggs were seen. The observer tried to turn the turtles over, but they proved to be too heavy. "Lots of turtles" were seen offshore. No signs of turtle tracks or digging could be found when the site was examined several days later. This, again, may have been due to the effects of windblown sand. It should be noted that the basking behavior previously mentioned almost always occurs on shore within a few yards of the water, and never 20-30 yards inland.

- —In the spring of 1983, a large turtle was seen during the early morning hours returning to the water at the west end of Polihua. The turtle's tracks were traced up the beach to a mound of sand (presumably a nesting site). The area was left undisturbed by the observer. A subsequent report indicated that a helicopter service from Maui used this same area of the beach to land tourists. The person who communicated the above information stated he is "convinced" that turtles are again nesting on Lanai.
- —During early August of 1983, a large turtle was seen during the daytime in the intertidal shoreline at Awalua, about 2 miles east of Polihua. The observer left the site to tell a nearby companion, but the turtle was gone when they returned.

Foraging Pastures

Rich coastal foraging pastures for green turtles are believed to occur along the northern and northeastern shores of Lanai. Gay (1965) mentioned that when he lived on Lanai, "turtles were plentiful along the windward side of the island." As quoted earlier, Kahaulelio (1902) said that: ". . . if one speared them at Polihua one caught several times four of them."

During the 1960's and early 1970's, green turtles were intensively captured off Lanai and Molokai for the restaurant trade and other commercial markets on Maui. Persons involved in this fishery commuted in small boats between Maui and the mostly remote coastal areas of Lanai. In 1968, a fisherman wrote on his monthly commercial catch report: "This area in 1948-1950 I used to catch at least 100 in 4 to 5 days fishing—for some reason there are no turtles there now." Another fisherman recently stated in a telephone interview that turtles caught during past years off Molokai could be recognized as having been ashore on Lanai's beaches by the tar stains on their undersurfaces.

Major algal food sources used by green turtles in Lanai's foraging pastures consist of *Amansia glomerata, Acanthophora spicifera,* and *Sargassum polyphyllum* (sometimes called "limu honu"). The sea grass, *Halophila hawaiiana,* has also been identified from the stomach of a 96.5-cm adult female green turtle speared by a fisherman in November 1978. This same animal was found to have large pieces of black and white plastic bags packed throughout its intestines (Balazs 1980).

On October 28, 1982, divers from Molokai visited Laewahie on Lanai's northern shore. An aggregation of green turtles was seen in about 6 m of water just west of a prominent ferroconcrete shipwreck. One of the turtles, a 56.5 cm juvenile, was captured by hand while it was sleeping under a ledge. The turtle was double tagged (No. 6569, 6570) and released (Bill Puleloa, pers. commun.).

The coastal foraging pastures of northern Lanai appear to be attractive habitat for the recruitment of young green turtles. For example, a 9-month old, 33-cm green turtle reared in captivity and released in 1974 off Oahu was speared 11 months later off northern Lanai. It was found with a group of other similar sized turtles. When the fisherman swam into view, all of the turtles fled except the captive-reared one (Balazs 1980).

Recommendations

No systematic surveys have been undertaken to ascertain the present status of sea turtles on the beach or in nearshore habitat of Polihua and the adjacent coastline. The effect of shifting sands from normally brisk tradewinds may be masking a greater level of nesting than is now being reported from chance sightings. Periodic nighttime searches by a trained observer need to be made from May through August to accurately quantify nesting activity. A series of scuba diving surveys should be carried out to gain a better understanding of the distribution and numbers of turtles dependent upon northern Lanai's nearshore habitat.

Literature Cited

Armstrong, R.W. (editor). 1973. Atlas of Hawaii. Univ. Press Hawaii, Honolulu, 222 p.

Balazs, G.H. 1975. Green turtle's uncertain future. Defenders 50(6):521-523.

____ 1978. Terrestrial critical habitat for sea turtles under United States jurisdiction in the Pacific region. 'Elepaio 39(4):37-41.

____ 1980. Synopsis of biological data on the green turtle in the Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-7, 141 p.

Beckwith, M. 1970. Hawaiian mythology. Univ. Hawaii Press, Honolulu, 575 p.

Emerson, N.B. 1915. Pele and Hiiaka: A myth from Hawaii. Honolulu Star-Bulletin, Ltd., Honolulu, 250 p.

Emory, K.P. 1924. The Island of Lanai: A survey of native culture. Bernice P. Bishop Mus. Bull. 12, 129 p.

Fornander, A. 1919-1920. Fornander collection of Hawaiian antiquities and folklore. Bernice P. Bishop Mus. Mem. 6(3):492-498.

Gay, L.K. 1965. True stories of the Island of Lanai. Mission Press, Honolulu, 83 p.

Kahaulelio, A.D. 1902. Fishing lore. *In* Ka Nupepa Kuokoa [Hawaiian Newspaper]. (Transl. by M.K. Pukui. Unpubl. manuscr. at the Hawaii Inst. Mar. Biol., Univ. Hawaii, Kaneohe, 89 p.)

Malo, D. 1951. Hawaiian antiquities. Translated from the Hawaiian by N.B. Emerson, Bernice P. Bishop Mus. Press, Honolulu, 278 p.

Pukui, M.K. 1983. 'Olelo No'eau: Hawaiian proverbs and poetical sayings. Bernice P. Bishop Mus. Spec. Publ. 71, 351 p.

Pukui, M.K., and S.H. Elbert. 1971. Hawaiian dictionary. Univ. Press Hawaii, Honolulu, 402 p. + additional 188 p.

Pukui, M.K., S.H. Elbert, and E.T. Mookini. 1976. Place names of Hawaii. Univ. Hawaii Press, Honolulu, 289 p.

Tabrah, R. 1976. Lanai. Island Heritage Ltd., Norfolk Island, Aust., 120 p.

Whittow, G.C., and G.H. Balazs. 1982. Basking behavior of the Hawaiian green turtle *(Chelonia mydas).* Pac. Sci. 36(2):129-139.

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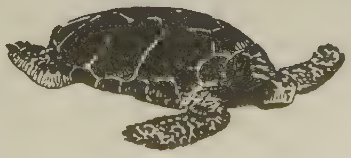

8508

TECHNIQUES

RETENTION OF FLIPPER TAGS ON HATCHLING SEA TURTLES

The inability of researchers to find a tag suitable for hatchling sea turtles has been mentioned repeatedly in the literature (Carr 1967*a*, 1967*b;* Hirth 1971; Hughes 1974; Carr et al. 1978; Mrosovsky 1978*b*, 1982, 1983; Rudloe 1979; Hendrickson and Hendrickson 1980). Body dimensions and weight increase substantially as a hatchling grows from a few centimeters long to an adult of 70 cm or more. This factor has been viewed as a major obstacle to devising a practical tag that will stay in place. Furthermore, an added demand on such a tag is the many years (10-60) that may be required for a turtle to reach adult size (Balazs 1979, 1982*b;* Limpus 1979; Limpus and Walters 1980; Mendonca 1981). A successful tag for hatchlings has considerable potential for answering important questions about survival rates, geographical dispersal, the "lost year" pelagic phase, early growth rates, and nesting site affinities. It would also help in evaluating hatchery and head-start projects attempting to replenish depleted turtle populations.

Existing published information on attempts to tag hatchlings with an external mechanical tag suggests that such a tag is "... soon either overgrown or popped off by the increasing thickness of the tissue it perforates" (Carr 1967*b;* see also Hirth 1971; Hughes 1974; Mrosovsky 1983). However, the details of the experimental evaluation leading to this conclusion have not been reported. Plastic tags have been used on the hind flipper (Carr 1967*b*) and carapace (Uchida 1973; Hughes 1974) of hatchlings released into the wild, but no recoveries have been reported, and shedding rates have apparently not been estimated through captive rearing. There is no specific mention in the literature of the use of metal tags on hatchlings. Metal flipper tags have been regularly used on adult sea turtles at nesting sites since the early 1950s.

Besides external mechanical tags, other marking techniques that have been tried on hatchlings include the internal implantation of small magnets (Carr 1967*b*) and stainless wire (Hughes 1974; Schwartz 1981), branding (Carr 1967*b*), tattooing (Carr 1967*b*; Balazs 1978), injection of europium (Shoop 1978) and autografts (Hendrickson and Hendrickson 1980). Some workers have also marked hatchlings by cutting away or notching marginal scutes (Bustard 1972, 1979; Hughes 1974; Limpus 1978). However, this technique has not resulted in reliable long-term recoveries. Furthermore, a potentially confusing situation has developed because hatchlings have been notched in many different research programs over the years. There are also inherent difficulties in distinguishing a notchmark from a natural injury (Mrosovsky 1978*a*).

An externally applied tag, such as a flipper tag, has substantial advantages over other marking techniques if it remains in place. These tags are far more likely to be recognized as a tag by the person resighting the turtle. They also permit a specific message to be visibly inscribed (i.e., return address, identification number) so that resighting data can be communicated back to the tagger.

A recent study in Hawaii of the shedding rates of metal flipper tags on small sea turtles indicates that this method of marking hatchlings should be seriously reconsidered. This note presents the results of the study, along with a discussion of its implications and requirements for further tag evaluation.

METHODS

In September 1980, hatchling green turtles, *Chelonia mydas*, were collected from French Frigate Shoals in the Northwestern Hawaiian Islands for use in testing a "living-tag" marking system involving autografts of contrasting pigmented tissue (Hendrickson and Hendrickson 1980). The hatchlings ranged from 5 to 6 cm in straight carapace length (SCL). Small Monel* tags (style 4-1005, size 1) from the National Band and Tag Co. of Newport, Kentucky were attached to the last right marginal scute of each hatchling to identify individuals during the study. These tags measure 8 x 2.5 x 2.5 mm when applied. They have been commercially available for many years, being advertised for use on fingerling fish, small mammals, and birds.

At 1 month of age, when the turtles ranged from 7 to 10 cm SCL, the tags had to be removed from the carapace due to distorted growth and necrosis of surrounding tissue. Replacement tags of the same size were then attached by the author to the trailing edge of the right front flipper. At 6 months of age (15-19 cm SCL) the same size tag was also applied to the left front flipper of each turtle.

Captive rearing of most of the turtles used for the living-tag study was completed at 12 months. The results of this work are reported elsewhere (see Hendrickson and Hendrickson 1981, 1983). The 174 surviving turtles averaged 23 cm SCL (range 16-30 cm) and 2.6 kg (range 0.7-5.2 kg). Each turtle was examined for the retention of flipper tags. At the same time, a larger Inconel® tag (size 681) was attached to a front flipper. Shortly thereafter, 169 of the turtles were released into the wild at several locations throughout the Hawaiian Islands.

RESULTS

Of the 174 yearling turtles, 147 (84.5%) still had both small flipper tags. One tag was missing from 26 (14.9%) turtles, and only a single turtle (0.6%) had lost both tags. Some tags were slightly corroded, but nearly all were still securely attached with little evidence of being overgrown or sloughing off (Fig. 1). Many tags had, however, rotated so that the long axis was perpendicular, instead of parallel, to the flipper's trailing edge. Of the 26 that lost 1 tag, 18 were from the right flipper applied at 1 month of age, and 8 from the left flipper applied at 6 months.

Five turtles were retained in captivity for continued rearing; four of these had two tags still in place, and one had a single tag. As of August 1983 when the turtles were 35 months old, three of the turtles that had both tags still attached at 1 year of age had each shed one tag. Of the other two turtles, one still had both tags, and one had the single tag that was present at 1 year of age (Table 1).

Two of the 169 turtles released have been resighted after a sufficient interval to yield further information on tag retention. Five others were reported washed or crawling

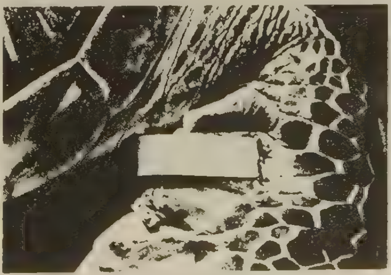

Figure 1. Size 1 Monel® and size 681 Inconel® tags on the right front flipper of a yearling Hawaiian green turtle. The size 1 tag was attached at 1 month of age.

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*Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

ashore during the first 2 months following release. The two longer-term resightings involved turtles 22 and 32 months of age. Both retained the two small tags present at the time of release. During their time in the wild, the turtles had grown from 29.5 to 33.6 cm, and from 27.2 to 36.0 cm. The 22-month old turtle was found speared just 3 km from its release site on the Island of Oahu. The 32-month old animal was released at the same site but was captured alive in a net 5,600 km away, at Truk, in the western Pacific.

DISCUSSION

Contrary to earlier reports, the external tags used in this study showed impressive retention rates. The success achieved is probably because small metal tags have not been fully tested on the front flipper. Another key factor may be that the tags used in the present study only showed minor corrosion. Corrosion is known to be an important factor in tag loss experienced in some research programs. Although long thought to be one of the better alloys available for turtle tags, Monel® is now known to corrode in a highly variable and sometimes severe fashion, even on turtles within the same population. If Monel® flipper tags were previously used on hatchlings by other workers, the tag shedding they observed may have been mainly due to corrosion. Tag corrosion and various other factors affecting tag retention have been discussed in Balazs (1982*a*).

Since late 1976, size 681 flipper tags made from Inconel®, an alloy far superior to Monel® in corrosion resistance, have been used on adult and immature green turtles in Hawaii. No corrosion has been seen in these tags, although some tags are still shed from tearing and other factors. Placing two or more tags on each turtle has greatly offset this problem (Balazs 1983). Inconel® tags are not currently available due to high production costs. However, a company in Western Australia (Stockbrands Co. Pty. Ltd. of Mt. Hawthorn) has recently offered titanium flipper tags at a reasonable price ($120 per 1,000). Titanium has nearly as high corrosion resistance as Inconel® (LaQue 1975). The author and C. J. Limpus (Queensland National Parks and Wildlife Service, Townsville, Australia) have arranged for the manufacture of titanium tags equivalent to the size 1 Monel® tags tested in the present study. Future evaluations on hatchlings will therefore be possible using a product that is superior to Monel® in corrosion resistance.

Previous workers tagging hatchlings often stressed the need for a tag to persist into adulthood. The protracted time to maturity, and the increasing level of research now being conducted on immature turtles in the sea, now seem to make this goal less critical. Similar information can probably be gathered by catching wild juveniles already tagged as hatchlings, and retagging them with larger tags as needed.

ACKNOWLEDGMENTS

Helpful comments on a draft of this note were provided by Larry Ogren, Harold Hirth, Nicholas Mrosovsky, and C. Kenneth Dodd.

Table 1. Growth and tag shedding of five green turtles retained in captivity from 12 to 35 months of age.

	Straight carapace length (cm)		Increase in growth (cm)	Size 1 tags	
	12 months	35 months		Right[1]	Left[2]
1.	20.9	41.8	20.9	Shed	On
2.	24.3	46.7	22.4	Shed	On
3.	20.0	40.2	20.2	On	Shed
4.	24.6	40.3	15.7	On	On
5.	22.0	41.4	19.4	On	[3]

[1] Tags initially put on at 1 month of age when the turtles ranged 7-10 cm SCL.

[2] Tags initially put on at 6 months of age when the turtles ranged 15-19 cm SCL.

[3] Tag not present at 12 months of age.

LITERATURE CITED

Balazs, G. H. 1978. Tattooing green turtles. Mar. Turtle Newsl. 8:3.

______. 1979. Growth, food sources and migrations of immature Hawaiian *Chelonia*. Mar. Turtle Newsl. 10:1-3.

______. 1982*a*. Factors affecting the retention of metal tags on sea turtles. Mar. Turtle Newsl. 20:11-14.

______. 1982*b*. Growth rates of immature green turtles in the Hawaiian Archipelago. *In* K. A. Bjorndal (ed.), Biology and Conservation of Sea Turtles. P. 117-125. Smithsonian Institution Press, Washington, D.C.

______. 1983. Recovery records of adult green turtles observed or originally tagged at French Frigate Shoals, Northwestern Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-36. 42 pp.

Bustard, H. R. 1972. Sea turtles. Taplinger Publishing Co., N.Y. 220 pp.

______. 1979. Population dynamics of sea turtles. *In* M. Harless and H. Morlock (eds.) Turtles: Perspectives and Research. Pp. 523-40. John Wiley and Sons, N.Y.

Carr, A. 1967*a*, No one knows where the turtles go. Nat. Hist. 40-43, 52-54, 56, 58-59.

______. 1967*b*. So excellent a fishe. The Nat. Hist. Press. 248 pp. Garden City, N.Y. (Note: Photo on dust jacket shows hatchlings on a beach with plastic tags attached to the hind flippers.)

Carr, A., M. H. Carr, and A. B. Meylan. 1978. The ecology and migrations of sea turtles 7. The West Caribbean green turtle colony. Bull. Amer. Mus. Nat. Hist. 162:1-46.

Hendrickson, L. P., and J. R. Hendrickson. 1980. "Living tags" for sea turtles. Report to Southwest Fish. Cent. Natl. Mar. Fish. Serv. Contract #80-ABH-00062, 20 pp. + Appendix.

______. 1981. A new method for marking sea turtles? Mar. Turtle Newsl. 19:6-7.

______. 1983. Experimental marking of sea turtles by tissue modification *In* Owens et al. (eds.) Western Gulf of Mexico Sea Turtle Workshop Proceedings, January 13-14, 1983. Sea Grant TAMU-SG-84-105. Pp. 30-31. Texas A&M Univ., College Station.

Hirth, H. F. 1971. Synopsis of biological data on the green turtle *Chelonia mydas* (Linnaeus) 1758. FAO Fisheries Synopsis No. 85. var. pag.

Hughes, G. R. 1974. The sea turtles of South-East Africa. II. The biology of the Tongaland loggerhead turtle *Caretta caretta* L. with comments on the leatherback turtle *Dermochelys coriacea* L. and the green turtle *Chelonia mydas* L. in the study region. South Afr. Assoc. Mar. Biol. Res. Invest. Rep. 36, 96 pp.

LaQue, F. L. 1975. Marine Corrosion: Causes and Prevention. Wiley Press, N.Y. 332 pp.

Limpus, C. J. 1978. The reefs. *In* H. J. Lavery (ed.) Exploration North. Richmond Hill Press, Victoria, Australia.

______. 1979. Notes on growth rate of wild turtles. Mar. Turtle Newsl. 10:3-5.

Limpus, C. J., and D. G. Walters. 1980. The growth of immature green turtles *Chelonia mydas* under natural conditions. Herpetologica 36:162-165.

Mendonca, M. T. 1981. Comparative growth rates of wild immature *Chelonia mydas* and *Caretta caretta* in Florida. J. Herpetol. 5:447-451.

Mrosovsky, N. 1978*a*, Editorial. Mar. Turtle Newsl. 8:1.

______. 1978*b*. Is notching hatchlings a reliable tagging method? Mar. Turtle Newsl. 8:2.

Mrosovsky, N. 1982. Editorial. Mar. Turtle Newsl. 22:1-2.

______. 1983. Conserving sea turtles. The British Herpetological Society London, 176 pp.

Rudloe, J. 1979. Time of the turtle. Alfred A. Knopf, N.Y. 272 pp.

Schwartz, F. J. 1981. A long term internal tag for sea turtles. Northeast Gulf Sci. 5:87-93.

Shoop, C. R. 1978. Europium tagging of green sea turtles. Mar. Turtle Newsl. 8:1-2.

Uchida, I. 1973. Pacific loggerhead turtle. Anima 1:5-17.

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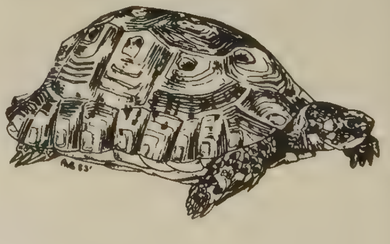

8509

SEA TURTLES AND DEBRIS: INGESTION AND ENTANGLEMENT

The impact of ocean debris on marine turtles was one of the many topics discussed at the recent "Workshop on the Fate and Impact of Marine Debris" (Honolulu, Hawaii, 26-29 November 1984). Short of severely curtailing the ocean dumping of all plastics, fishing gear and other material, there is probably not much that can be done to lessen the adverse effects of man-made debris on sea turtles. There are, however, a number of immediate activities that could be undertaken to improve our understanding of the nature of the impact. The following recommendations were made at the workshop:

1. There should be greater efforts worldwide to record stranded turtles and conduct necropsies aimed at documenting debris ingestion and entanglement.
2. Studies should be conducted that involve the controlled feeding of plastics and other debris to turtles in captivity in order to gain definite information on intestinal obstruction, absorbtion of plasticizers, and feeding behavior.
3. Field studies aimed at elucidating the pelagic life of sea turtles along drift lines should be undertaken north of the Hawaiian islands in the Pacific.
4. A more thorough assessment should be made of sea turtle interaction with jettisoned by-catch from shrimp trawlers and other fisheries.

Based on an extensive literature review and personal communication with other researchers, I tabulated 64 cases of ingestion and 55 incidents of entanglement, many of which involved more than one turtle. In a continued effort to maintain a file on sea turtles ingesting or becoming entangled in marine debris, I would greatly appreciate receiving reports (old or new) of any such occurrences at the address below.

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8510

STATUS AND ECOLOGY OF MARINE TURTLES AT JOHNSTON ATOLL

BY

GEORGE H. BALAZS[1]

INTRODUCTION

The aim of this paper is to consolidate all available information on marine turtles at Johnston Atoll, and to present the results of a short-term tagging study recently conducted there. The importance of this work rests on the fact that it has never been done before, that marine turtles are listed under the U.S. Endangered Species Act (since 1978), and the atoll is a National Wildlife Refuge. The Defense Nuclear Agency has operational control of Johnston with the primary mission of maintaining nuclear readiness for the resumption of atmospheric testing, should it be so directed. Several other organizations are present under Defense Nuclear Agency stewardship, including an Army chemical storage facility, a Coast Guard loran station, a NOAA weather station, and a civilian support contractor, Holmes and Narver, Inc. The U.S. Fish and Wildlife Service in Honolulu cooperatively manages the area as part of the National Wildlife Refuge System.

Johnston Atoll is located at lat. 16°45'N, long. 169°31'W, and is one of the most isolated atolls in the world. The land area consists of four islands (Johnston, Sand, Akau, and Hikina) totaling only about 2.8 km^2, most of which is man-made. The surrounding reef covers an area 11 by 22 km. Johnston is one of the best studied atolls in the central Pacific, due to its small size and extensive use for military purposes over the past 45 years. A comprehensive summary of the atoll's natural history, including all known scientific studies up to 1973, has been compiled by Amerson and Shelton (1976). The ecological significance of the atoll is described separately in this publication (p. 361-368) by four prominent ecologists.

Much of the previous research conducted at Johnston has been on the terrestrial fauna and flora, with major emphasis on seabirds. The studies on the marine environment and biota have been mainly centered in the lagoon. Virtually no work has been done off the south shore of Johnston Island. This has been due in part to safety and security restrictions, and poor diving conditions. Since most of the turtles found at the atoll occur in this region, it is perhaps not surprising that they have received so little attention over the years.

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The Army plans to construct a large-scale incineration facility on Johnston Island to destroy chemical agents and munitions stored there. The storage bunkers are along the south shore of the island adjacent to West Peninsula, the site where the plant will be constructed. Comprehensive information on this project, Johnston Atoll Chemical Agent Disposal System (JACADS), has been presented (U.S. Army Corps of Engineers 1983). Construction of the facility is planned to begin in late-1985, and take 3 years to complete. The number of personnel on the island will double from the present 350. Factors that have not yet been decided, or are classified for security reasons at present, include the life of the facility, the total number and kinds of munitions to be incinerated, and the disposition of certain nontoxic byproducts. Initially, at least 72,000 rockets containing 345 metric tons of nerve agent (GB and VX) are scheduled to be processed.

This paper is the culmination of work commissioned by the U.S. Army Corps of Engineers, Pacific Ocean Division, to obtain baseline data on marine turtles at Johnston Atoll. The study was prompted by the absence of information on these reptiles, their protected status under Federal law, and the proximity of the JACADS project. Recommendations given in this paper will help ensure the conservation of Johnston's turtles, as requested in the terms of reference for the study.

HISTORICAL OVERVIEW OF TURTLES

There are few accounts of sea turtles at Johnston Atoll in the literature. Amerson and Shelton (1976) summarized, as follows, all information known to them as of late 1973 (p. 112):

> "Reptiles, Species Accounts - There are no general references that illustrate the reptiles of Johnston Atoll. Taxonomy of the turtles follows Carr (1972) and Amerson (1971).
>
> "BLACK SEA TURTLE *Chelonia agassizi*
>
> "*Status* - Regular uncommon visitor; known from the lagoon, offshore Johnston Island, and Sand Island.
>
> "*Observations* - Brooke (MS.), who visited Johnston Atoll in March 1859, commented about the lack of turtles: 'The reefs are covered with fish of various kinds. Mullet abound, but there are no turtles.' Wetmore (MS. a and b) likewise, recorded no turtles at Johnston Atoll in July 1923.
>
> "POBSP [Pacific Ocean Biological Survey Program] personnel recorded sea turtles in the shallow marginal reef area west of Johnston Island in July 1963. An adult (USNM 163581) was collected 20 November 1966 on the beach of Sand Island. Island personnel in 1973 reported seeing 10 to 12 turtles offshore of Johnston Island throughout the year. A longtime resident estimated harvesting 12 to 15 per year.
>
> "*Annual Cycle* - The Black Sea Turtle apparently visits Johnston Atoll year-round. No records exist of it breeding on the atoll, although

> perhaps it did in small numbers prior to inhabitation by man. This species breeds during the summer in the northwestern Hawaiian Islands, especially at French Frigate Shoals (Amerson, 1971)."

The validity of the species account by Amerson and Shelton (1976) will be a subject of discussion later in this report.

In December 1892, Captain John Cameron of the schooner Ebon stayed at Johnston Atoll for a month after sailing directly from Laysan Island in the Northwestern Hawaiian Islands. The account of this visit (Farrell 1928) mentions sea turtles, but was not cited by Amerson and Shelton (1976). The relevant sections of Farrell (1928) are as follows (p. 402-405):

> "Our first call was at Johnston or Cornwallis Island, five hundred and sixty miles south of Laysan and southwest of the eight islands of Hawaii proper. We found a good berth in its lagoon, and in a pretty little cove, on a beach of white sand, was an ideal spot for our tent. Near by were ruins of shanties built years before by a guano company; there also was a well, with pumps and pipes intact, which we cleaned and put in order.
>
> "Signs of men, signs of shipwreck! We stumbled across two boats, both hauled above high water, one in fair condition, the other badly smashed; and in the craft were harpoons and lances and some bird shot in bags. The condition of the better boat, which was well worth the repairs I decided to give it, indicated that the men who left it there had been rescued. Else why should they have abandoned a tolerably seaworthy craft on a desert island?
>
> "Our catches of sharks at Johnston were only fair, because our bait was principally sea birds, which the brutes did not relish as they had the flesh of hair seals; but our hauls almost filled our containers with liver oil. Now and then we took things more easily: 'Spell O!' was passed, and we hunted turtles. One of the men employed the Kusaie method of taking them by anchoring a few captive females near the beach to attract the bulls. It succeeded admirably and helped us greatly with attractive bait for shark fishing.
>
> "We were standing to sea, bound to Fanning Island, when from the mate, who was at the masthead, came a cry of 'Sail O!' A bark under full sail was heading for us. Through the telescope we could see that she was a whaler: that was made evident by boats hanging from her davits ready for immediate use. I lost no time in pulling to her with some turtles and two pigs, welcome additions to the fare of a vessel long at sea and especially for Christmas dinner, as the day was December 24."

Votaw (1943) included some of Captain Cameron's comments about turtles in a short historical paper on Johnston Atoll. Turtles were also mentioned, but again not cited by Amerson and Shelton (1976), in a Honolulu newspaper article by Benson (1953). Describing the dynamiting necessary from 1939 to 1942 to clear out coral heads in the lagoon, Benson (1953) stated that:

> "Interest was added to the process by the presence of numerous huge sharks. There was one monster in particular who demonstrated his prowess one day by swallowing a sea turtle - whole - at one gulp."

In recent years, sea turtles at Johnston Atoll have been discussed by Balazs (1978, 1980b, 1980c, 1982d). Two of these papers (Balazs 1980b, 1982d) made recommendations that stressed gathering baseline data on this little-known and isolated turtle population. A brochure describing National Wildlife Refuges in the Pacific briefly mentions that the green sea turtle is among the marine life found at Johnston (U.S. Fish and Wildlife Service, MS.).

Except for the single specimen in the U.S. National Museum listed by Amerson and Shelton (1976), there is no indication of scientific personnel having examined, tagged, or studied sea turtles at Johnston Atoll. Starting in 1978, turtle sighting report forms have been sent to resident personnel at the atoll, but only limited information could be acquired by this method (Balazs 1982d). Casual observations and counts of turtles from shore have recently been recorded in trip reports by Ludwig (1982), Ludwig et al. (1982), and Nitta (1982). Applied Eco-Tech Services (1983) included a discussion of turtle sightings in their consultancy report on water quality.

ASSESSMENT METHODS

Two field studies, totaling 28 days, were conducted at Johnston Atoll to accomplish the assessment. The first phase of study was September 29-October 13, 1983 and involved two workers. The second phase was November 3-17, 1983 involving five workers. In addition, a preliminary 2-day planning visit was made by one worker on August 30-September 1, 1983.

Capture Efforts

Efforts to capture turtles alive and unharmed were undertaken using large-mesh tangle nets, scoop nets, and scuba to facilitate capture by hand. All three of these methods have been successfully employed to study green turtles in coastal waters of the Hawaiian Islands (Balazs 1976, 1982b).

The tangle nets were made of 2-mm diameter nylon line, with a stretched mesh of 46 cm (23 cm square mesh), and a depth of 3.5 m. The length of the nets ranged from 9 to 40 m. The nets were set at the surface extending vertically through the water column. They were deployed and retrieved close to shore using a small boat at sites recommended by resident personnel, or where turtles were seen foraging or in transit. Up to five nets were set at one time at different locations. All nets were checked from land with binoculars every 1-2 h diurnally to see if a turtle had been caught.

Large scoop nets were used by approaching turtles at the surface with a boat. Efforts with scuba were directed at locating and catching turtles by hand during the course of underwater surveys.

Following their capture, turtles were taken ashore for tagging and examination for a period requiring up to 2 h. Before being released, color photographs were taken to help document morphological features.

Tagging and Body Measurements

Turtles were tagged for long-term identification with numbered Inconel[2] alloy tags, size 681, custom made by the National Band and Tag Company of Newport, Kentucky. Balazs (1980c, 1982a, 1983) describes the history of these tags used in Hawaii and their superior corrosion resistance compared with Monel alloy. The tags measure 25 x 9 x 8 mm, weigh 3.5 g, and are self-piercing and self-locking when applied with special applicators. Depending on the turtle's size, from two to five tags were applied to offset tag loss. Tagging sites were the trailing edges of both front flippers in the webbing between the third and fourth scales counting proximal to distal, in the axillae close to the first scale, and on a hind flipper on the inside trailing edge well under the carapace. A secondary and potentially long-lasting mark in the edge of the carapace resulted from the bone biopsy (described later).

Short-term visual recognition of tagged turtles after their release was made possible by painting a white number on each side of the carapace using Dupont Lucite spray paint. Based on studies elsewhere, it was estimated that these numbers would remain visible for at least 10 days.

Observations on the turtles consisted of: straight-line (SCL) and curved (CCL) carapace length from the center of the precentral scute to the posterior tip of a postcentral scute; straight-line carapace length from the center of the precentral to the notch between the postcentrals; straight-line and curved carapace width at the widest point (the sixth marginal scute); straight-line plastron length along the midline; straight-line head width at the widest point; tail length from the posterior rigid edge of the plastron to the tip of the tail; straight-line flipper width from the claw scale to the sixth scale on the trailing edge; and body weight.

Food Sources and Epizoites

Food sources were determined by sampling the turtles' stomachs with a plastic tube inserted through the esophagus. Small amounts of water were introduced and aspirated to obtain food material. In addition, unswallowed particles of food were removed from the mouth, and fecal material that could be collected was rinsed to isolate incompletely digested food. These three field techniques for sampling dietary components are discussed in detail in Balazs (1980a). Observations made of turtles feeding at specific sites also permitted the direct collection of algal forage during underwater surveys.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Food items were preserved in dilute Formalin and identified to the lowest taxon possible. Frozen bulk samples collected from the foraging habitat were biochemically analyzed to determine major nutrients and mineral composition.

Epizoites found on the skin and hard parts of the turtles were scraped off, preserved in dilute Formalin, and identified to the lowest taxon possible.

Biopsies and Blood Sampling

Biopsies of bone and lamina were taken with a saw by cutting a small triangular piece from the edge of the 10th left marginal scute. Depot fat was sampled from directly under the skin by making a 2-3 cm incision in the inguinal region. Tissue sampling procedures described by Rainey (1981) and Menzies et al. (1983) were used as a guide for this work. Bone and fat samples were frozen in glass vials and stored for future analyses of radionuclides and heavy metals.

Blood collection followed the methods described by Owens and Ruiz (1980) and Bentley and Dunbar-Cooper (1980). A needle and syringe were used to draw blood from the paravertebral sinus on either side of the midline of the dorsal neck surface. The blood was centrifuged and separated into packed cells and serum. Sera were frozen and analyzed for testosterone levels to determine sex. Packed cells were refrigerated and analyzed within a few hours for cholinesterase activity. The 17-Minute Manual Method, routinely used at the Johnston Island medical facility to detect anticholinesterase intoxication in humans, was used for analysis of turtle blood.

Underwater Surveys

Underwater scuba surveys were made to census turtles, locate and assess prominent foraging and resting habitat, and gather other ecological data. Two or three divers working together within visual range carried out the surveys. All surveys took place during the daytime.

Terrestrial Surveys

Terrestrial surveys were conducted along the coastlines of all four islands for the purpose of locating possible nesting and basking habitat. Systematic observations from shore were also made of coastal waters.

Personal Interviews

To compile anecdotal information, fishermen and divers, especially those who have been at Johnston for many years, were interviewed. Requests were also made to examine photographs in private collections showing turtles caught during past years.

Literature Search

The published and unpublished literature pertinent to Johnston Atoll was reviewed. This search included articles in the two major Honolulu newspapers. All known historical reference to turtles at the atoll have been presented in the previous section of this report. However, the literature review also encompassed articles on perturbations to the environment that could be of significance to turtles or their habitat.

An inquiry was made to the U.S. National Museum (Washington, D.C.) to obtain further data on the specimen mentioned by Amerson and Shelton (1976) as having been collected in 1966 "...on the beach of Sand Island."

FINDINGS

Results of Capture Efforts

A total of 21 turtles were captured (Table 1). All were green turtle, Chelonia mydas, taken with nets, and no repeat captures were made. There were no scars indicative of old tags being shed. No turtles were caught with scoop nets or by hand, due mostly to turbid water conditions and the rapid diving behavior of the turtles when approached by boat. The locations selected for the nets were exclusively off the south shore of Johnston Island (Fig. 1). Nearly all of the turtles sighted during the surveys were in this area. The high concentration along this side of the island was also confirmed by everyone interviewed. The water off the south shore is silt-laden resulting in poor underwater visibility. Reasonably good water clarity was found at other sites in the atoll.

The daily netting effort at each location, expressed in meter-hours (MH) (length of net by hours fished), is shown in Table 2. During phase 1 of the field study, nets were regularly set at locations 1-5 and left both day and night. However, this sampling procedure proved unworkable because of the high incidental capture of eagle ray, Aetobatus narinari, and large manta ray, Manta birostris. The entanglement of rays occurred only at night or during twilight hours. Once caught, manta rays were able to twist with such force that sections of the net became snarled and useless. Eagle rays caused less of a problem, but were still able to pull sections of floatline underwater and hold them there. Most turtles caught with rays under these conditions would have drowned. During the times the nets were left out at night, only one turtle was caught, apparently at morning twilight (Table 3, tag No. 7451). Although eagle rays were also in the net, the turtle escaped injury due to its large size and place of entanglement away from the rays. All netting during phase 2 was conducted diurnally (Table 2) to eliminate the problem of accidentally catching rays. Shore observations during the daytime indicated that at least some turtles avoided the nets. Avoidance would probably not have been possible at night.

Nets were set at 17 sites, but turtles were caught at only 4 of them (Table 1). Three of these locations (1, 2, and 3) were close to or immediately east of the West Peninsula, and one location (7) was between West Peninsula and the southwest corner of the island (Fig. 1). Eight of the 21 turtles were caught at location 2; 5 each were caught at locations 1 and 7; and 3 were caught at location 3. Catch per unit effort was considerably better at locations 2 and 7 (589 and 550 MH per turtle, respectively; Table 1). A similar catch per unit effort was obtained during phase 1 and phase 2 field studies (1,123 and 1,197 MH), although twice as many turtles were caught during phase 2 (14 versus 7).

Species Present

The turtles captured displayed no clear characteristics that would justify their designation as _C. agassizi_, the black turtle of the east Pacific. The large size of the adults, the contour of the carapace, and the color of the plastron were all mostly consistent with _C. mydas_. An exception was a specimen that had a strongly tapered posterior to the carapace, and a moderate amount of gray pigment in the ventral surface of the marginal and postcentral scutes (tag No. 7551). These features are pronounced in _C. agassizi_, including dark pigment throughout much of the plastron. This turtle therefore seems to be intermediate between _agassizi_ and _mydas_. None of the other turtles captured, nor those remembered by Cris Balubar, a resident employee and former turtle fisherman, had dark pigment in the plastron.

Carapace color and pattern varied considerably, ranging from predominantly tan with brown radiations (tag No. 7451) to olive with black flecks (tag No. 7517). When seen in the water before capture, the carapace of most turtles at Johnston is masked by a layer of silt. Carapace coloration within other green turtle populations, such as in Hawaii, is known to vary with stage of maturity, sex, and possibly even environmental factors (Balazs 1980c). However, the carapace and dorsal skin surface of adult _C. agassizi_ is always predominantly black.

The observation by Amerson and Shelton (1976) that the black turtle occurs at Johnston is invalid based on findings of this present study. Amerson and Shelton's (1976) nomenclature appears to have been founded almost completely on their citation of Carr (1972), who stated (p. 25):

> "...The black turtle of the eastern Pacific lacks the numbers to withstand that abuse, and may well become an incidental casualty along the American mainland shores. To my eye, however, the black turtle stock occurs elsewhere--in the Galapagos Islands, among the mid-Pacific Islands, and in parts of the Indian Ocean. With its range extending through so much territory, the complete loss of the Mexican and Central American colonies might not obliterate _Chelonia agassizi_; but here again, the name, as I am using it, surely covers a number of hitherto unnamed races. The sooner these are properly defined, the sooner concern over their plight will be generated."

No other species of sea turtle was seen during the field studies. An unverified sighting of a hawksbill turtle, _Eretmochelys imbricata_, is listed by the U.S. Army Corps of Engineers (1983). In addition, four turtles, thought to be hawksbills, were reported in shallow water off the northeast corner of Johnston Island in September 1980 (R. J. Novak in litt. to G. H. Balazs). Cris Balubar and others interviewed indicated that only green turtles have ever been seen by them within the atoll.

The leatherback turtle, Dermochelys coriacea, has been observed on several occasions by personnel trolling for fish outside the atoll. Cris Balubar saw one about 11 km to the north of the atoll. In 1981, a large decapitated (but still moving) leatherback was seen, apparently after being accidentally hit by a boat. Efforts to gaff the turtle and bring it aboard proved unsuccessful.

Population Structure

Body measurements and weights presented in Tables 3, 4, and 5 indicate that 60% (14) of the turtles captured were mature adults. Turtles <82.9 cm SCL were estimated to be immature (see Balazs 1980c for a discussion of size categories). The proportion of adults in the Johnston population is therefore substantially greater than at coastal areas studied in Hawaii. At a comparable foraging area on Molokai, Hawaii only 9% of 81 green turtles sampled with nets were adults. The sighting of turtles during surveys at Johnston, along with information resulting from interviews, confirmed that the population is composed of mostly large turtles. The smallest turtle captured was 57.4 cm SCL; however, a few others estimated to range down to 35 cm SCL were seen during the surveys.

The age structure and growth rates of turtles at Johnston are presently unknown. In the Hawaiian Islands, green turtles are estimated to take 11-59 years to grow to an adult. Growth rates have been found to differ significantly among resident foraging areas within the archipelago (Balazs 1982b). The high percentage of adults at Johnston could be caused by several factors, including rapid growth rates, low recruitment of small turtles to the population, high predation and mortality of small turtles, and low predation and mortality of adults.

The 15 turtles that were weighed ranged from 63.6 to 151.4 kg (Table 5). The mean weight of three adult males was 104.8 kg (range 84.5-115.9 kg). The mean weight of six adult females was 112.0 kg (range 87.7-115.4 kg). The largest turtle ever caught by Cris Balubar was a 186 kg male.

Testosterone levels were determined from blood samples of 12 turtles for sex determination. The sex of six other turtles, all adults, could be determined by external features (i.e., a long, large tail for males). The sex ratio of this 18-turtle sample was 2.6:1 in favor of females (Table 6). If only immature turtles are considered, the ratio was still 3:1 in favor of females. Of special interest among the immature turtles was a fairly large specimen (79.1 cm SCL, 74.1 kg) that still had a short tail (18.2 cm). The testosterone level showed this turtle to be a male.

Abundance and Distribution

Capture and tagging efforts were focused at principal aggregation sites of turtles. Seven turtles were tagged during phase 1 from this area. After an interval of 20 days, phase 2 capture efforts yielded 14 more turtles, none of which had been tagged earlier. Because no recaptures were made, these data alone do not permit an estimate of the number of turtles present along Johnston Island's south shore.

Only one paint-marked turtle was resighted. This turtle was observed at the surface near dive location I (Fig. 2) by a resident employee sailing a Hobie cat. The turtle dove vigorously when approached. Turtles have been occasionally seen in this general area, which consists of a dredged turning basin and ship channel along the eastern portion of Johnston Island's north shore. This turtle (tag No. 7485), had been captured 6 days earlier on November 6 at net location 2, and released shortly thereafter at the port facility on the north shore (Fig. 1). All 7 turtles captured during phase 1 and 12 caught during phase 2, were released at this site. The other two turtles (tag No. 7560 and 7565) from phase 2 were transported by truck and released at the south shore. The short distance (2 km) around the island, in relatively calm water between the north and south shores, should not have presented an obstacle to the turtles. Biotelemetry has shown that immature green turtle have a well-developed homing ability on their resident habitat (Ireland 1979a, 1979b). Furthermore, adults can find their way across hundreds of kilometers of ocean when migrating between resident areas and nesting beaches (Hirth 1971; Carr 1972).

Only three turtles were seen during 26 diving surveys with scuba totaling over 22 h, or 46 man-h, of bottom time (Fig. 2). All three turtles were swimming when sighted. While it was not possible to approach close enough to capture them, the turtles nevertheless did not flee in the manner seen when encountered by boat at the surface. The turtles were sighted at dive locations D, J, and P off the south shore in the same general area where nets were set. Most of the dive surveys (18 of 26) were made here, but poor underwater visibility, ranging from at best 10 m to as low as 1.5 m, greatly limited the possibility of seeing swimming turtles. However, careful systematic searches of the bottom were made at all locations to find places where turtles were sleeping, hence less liable to flee from a diver. None was found, although most areas surveyed, from just several meters offshore out to 1.8 km (dive location U), appeared well suited as sleeping habitat. Sleeping sites repeatedly used by green turtles have recognizable marks in the substrate. Except for two possible minor sites at dive locations C and P, no habitat was found showing such usage. The major sleeping areas for turtles along the south shore remain undiscovered, but it seems unlikely they are commuting very far.

As shown in Figure 2, no diving surveys were made to the southwest of West Peninsula in the waters downwind of the sewer outfall. In addition to raw human sewage, the outfall discharges wash water from the decontamination procedure used at the chemical storage facility. Other effluent, a dense black discharge, was regularly seen from shore during phase 1. This was reported to result from flushing of old sewer lines. The discharge point of the sewer outfall is immediately southwest of dive location J (Fig. 2). No turtles have been seen underwater during the few dive surveys previously made downwind of the outfall (Ludwig et al. 1982; Applied Eco-Tech Services 1983). However, from shore, turtles are commonly seen in this area while at the surface. It is possible that the sleeping areas are located somewhere along here. Recreational swimming and scuba diving are not permitted in waters off the entire south shore of Johnston Island.

Sightings of individual turtles at the surface, other than along Johnston's south shore, were made once at dive location O, and four times in the ship channel at the east end of Johnston Island. In addition, three immature turtles were seen over the tops of coral heads in the vicinity of dive location X. No turtles were seen in coastal waters by observers placed on Akau and Hikina Islands from 0800 to 1700 on November 10, and at Sand Island from 0800 to 1700 on November 11. No turtles were seen during snorkel surveys made by two observers for 80 min on November 9 in shallow water off the east and north end of Sand Island. No turtles were seen by two observers during 30 min of observation on October 12 from the abandoned tower near dive location L. These findings, which suggest low numbers of turtles and sparse distribution at sites other than Johnston's south shore, are consistent with information gathered during interviews. For example, Armyman Tim Snover stated that, over the past 10-month period, he had never seen a turtle during six scuba and eight snorkel dives in the northern portion of the atoll at Donovan's Reef (Fig. 2). Other personnel have seen turtles there, but only occasionally.

The reports of turtles in abundance along Johnston's south shore, and especially off West Peninsula, contrast sharply with the low numbers seen elsewhere in the atoll. For example, Ludwig (1982) saw an estimated 30 turtles during 1 h of observation from West Peninsula at 1800 on September 15, 1981. Up to five at a time were seen around the tops of individual coral heads. When Ludwig (1982) visited here again on September 17, he spotted eight turtles during 30 min. Ludwig (1982) also reported that personnel frequently visit West Peninsula to watch turtles. During 3 days in July 1982, Nitta (1982) saw 8-11 turtles while viewing from West Peninsula in the late afternoon. Applied Eco-Tech Services (1983) made the following comments from surveys conducted along the south shore during June 2-11, 1983.

> "Although the survey team was not directing their efforts to turtle observations, nearly every head bearing Bryopsis was seen to have one to perhaps four specimens of Chelonia mydas in the immediate vicinity....Upon sighting the dive boat, these turtles would sound rapidly, move away from the area and resurface 20-40 m away. This behavior and the uncertainty of the general movements of the turtle population during the course of the day precludes an accurate estimate of the total number of turtles present off the south shore at any given time. The algae survey team typically noted 20-25 turtles during each morning's efforts (3 h) and a similar number during each afternoon. It should also be noted here that this estimate is conservative since it represents sightings of surfacing animals only, the water clarity being sufficiently poor to prevent sightings of submerged organisms."

At the beginning of phase 1, four to six turtles were commonly sighted off West Peninsula, usually within a few hours of high tide. However, the number spotted varied considerably (0-13) while motoring along the entire south shore at various times throughout the study. These counts were undoubtedly influenced by tide stage, changes in visibility due to sun angle, and probably a greater awareness by the turtles of an approaching boat. At the end of phase 2, on November 16, an observer was stationed at West Peninsula for an hour during an incoming high tide. No fewer than five and possibly as many as eight turtles were seen; none of which appeared to have painted numbers. These data suggest there may be a considerable turnover in turtles using the area, and that the total number may be many times larger than what can be seen during a several day period.

Food Sources

Samples of stomach contents, mouth contents, or feces were acquired from 13 of the 21 turtles captured. Stomach contents from eight turtles contained five kinds of benthic algae, diatoms, filamentous bacteria, unidentified fibers, and a single amphipod (Table 7). The green algae, *Bryopsis pennata* var. *secunda*, was prominent in samples from three turtles and *Caulerpa racemosa* var. *uvifera* prominent from one turtle. All other items were present only in relatively small or trace amounts. Mouth contents from five turtles contained five kinds of benthic algae (including unidentified blue-green algae), diatoms and a single amphipod (Table 8). A stomach sample had already been taken from one of these turtles and the mouth contents were identical. Of the four turtles sampled only for mouth contents, *B. pennata* var. *secunda* was prominent from two *C. racemosa* var. *macrophysa* prominent from the other two. Identification of fecal contents from the single turtle sampled revealed a composition of 75% *C. racemosa* var. *uvifera*, and 25% *B. pennata* var. *secunda* (Table 8). Differences in the digestibility of the two species could have affected these percentages, therefore, the actual ratio ingested is unknown. Based on the limited sample data presented for stomach, mouth and fecal contents, the size of the turtle does not appear to be a factor in the kind of alga eaten. The turtles' major food sources (*Bryopsis* and two varieties of *Caulerpa*) grow in prime foraging habitat near the West Peninsula. Turtles were commonly seen surfacing and diving in typical foraging behavior over coral heads having dense *Bryopsis*. Interestingly, *Bryopsis* is not among the 56 known species of algae used as food by Hawaiian green turtles, nor has it been recorded anywhere else as green turtle forage. However, *C. racemosa* is eaten at several locations, but seems to be poor forage yielding very slow growth rates in green turtles (Balazs 1980c, 1982b).

Cris Balubar stated that the turtles he recalls cutting open and cleaning only contained the two common types of seaweed (*Caulerpa* and *Bryopsis*) found along the south shore of Johnston Island.

An unidentified cuboidal jellyfish (Cubomedusae) was abundant along Johnston's south shore during the early part of phase 1. The bell of these animals measured about 13 cm long. Many of them settled into the numerous depressions between coral heads where torn pieces of *Bryopsis* also collected. No evidence was found that green turtles feed on these jellyfish. However, other hydrozoans, such as *Physalia* and *Velella*, are eaten on an opportunistic basis by green turtles in Hawaii (Balazs 1980c).

Kitchen waste is dumped into the ocean daily at the southwest corner of Johnston Island. Pritchard (1982) reports that some green turtles scavenge regularly for food scraps discarded in a similar manner at the military facility on Kwajalein Atoll. No evidence was found that this food source is utilized by turtles at Johnston.

The circumstances in which a fecal sample was collected from a turtle (Table 8) are of interest. This turtle was captured at net location 7 at 1700 h on November 8 along with another turtle (Table 3). A section of the net had become snagged on a nearby coral head, thus preventing it from reaching the surface to breathe. The turtle was comatose when recovered. Except for contraction of the tail when pulled straight, there were no signs of life. Periodic compression of the plastron for 1 h in an attempt to ventilate the lungs gave no apparent results. The movement of air by this method seemed to only take place through the esophagus, since the glottis remained tightly closed. A small diameter plastic tube was therefore pushed though the glottis to hold it open and afford passage of air. The lungs were then gently ventilated by blowing into them at irregular intervals for the next hour with the turtle in a prone position. The turtle raised its head and opened its mouth to breathe for the first time after being seemingly lifeless for over 2 h. The tube was removed as breathing gradually became more frequent, and movement of the flippers resumed. The turtle was subsequently left prone overnight to give it more time to recover before release. In the morning, 1.5 kg of fecal matter were found to have been passed. The turtle swam off and dove in a normal manner when released.

Foraging Habitat

The principal foraging habitat for turtles at Johnston Atoll consists of a narrow band of heterogeneous algal pasture immediately off and along the south shore of Johnston Island. To a lesser extent, this feeding zone also exists contiguously on the northeast side of the ship channel (dive location X, Fig. 2), where Bryopsis alone is present on the tops of coral heads. Based on published literature, personal interviews, and surveys conducted during the present study, the standing crop densities of benthic algae suitable as forage for green turtles are extremely low at most all other sites in the atoll. Many kinds of benthic algae occur at Johnston (Brock et al. 1966, Buggeln and Tsuda 1966, 1969; summarized by Amerson and Shelton 1976). From this literature, Balazs (1982d) previously noted that C. racemosa, Codium arabicum, and Gelidium pusillum might serve as algal forage for Johnston's turtles, since green turtles elsewhere feed on these three species. However, the apparently sparse quantities of the latter two species negate any significant benefit that could be derived. There are small areas of Caulerpa racemosa var. uvifera in shallow water around Sand, Hikina, and also possibly Akau Island that could be used by turtles, but no turtles were seen feeding at these locations.

Four kinds of benthic algae collected during diving surveys along Johnston's south shore comprise nearly all of the standing crop that exists there (Table 9, dive location J). Three of these, B. pennata var. secunda, C. racemosa var. macrophysa, and C. racemosa var. uvifera, were identified as major food sources from the stomach, mouth, and feces of turtles. The fourth alga, C. serrulata (Förskal), was commonly seen in many areas close to the south shore, often growing in proximity to the two varieties of C. racemosa. Since C. serrulata was not found in any of the food samples, the turtles must be actively ignorning this species. Such an aversion could be due to metabolites known to be present in some Caulerpa that can act as toxic feeding deterrents (Paul and Fenical 1982; Paul 1983). This deterrence has not been demonstrated in turtles, but the subject warrants investigation. Certain algae of the Order Caulerpales are food sources for green turtles at a number of locations worldwide. More than 100 species are known, and at some atolls in the Pacific very dense populations of the algae are present (Meinesz et al. 1981).

Bryopsis and the two varieties of C. racemosa sampled fresh from foraging habitat off West Peninsula were found to differ considerably in nutrient composition (Table 10). Bryopsis contains 2 to 3 times as much protein as Caulerpa, and only about 60% the ash content. Bryopsis also has 2 to 4 times greater lipid content (ether extract). It should be noted that the protein percentages shown in Table 10 were obtained by a standard analytical procedure used for terrestrial forage (proximate analysis), where total nitrogen is multiplied by a value of 6.25. This may be an overestimate for certain marine benthic algae. For example, Dawes and Goddard (1978) measured protein in C. racemosa (variety not stated) from Florida by a direct protein extraction technique that gave a content of 4.8%. Protein content for racemosa in the present study was calculated to be 8.0% (for uvifera) and 9.1% (for macrophysa).

The nutrient composition of Bryopsis collected from two different environments is also presented in Table 10. In one, Bryopsis was sampled off the top of a coral head where turtles were commonly seen feeding. The other collection was made nearby from a depression between coral heads where drifts of naturally torn Bryopsis had collected due to low water movement. Bryopsis in these depressions is not visible from the surface due to high turbidity. Consequently, it is unknown if turtles ever feed on this loose material. It was theorized that attached Bryopsis repeatedly cropped by turtles might contain higher protein and less fiber (complex polysaccharides) due to the constant new growth taking place at the grazed ends. Protein levels shown in Table 10 do not support this hypothesis, since the loose material is almost 2% higher (25.7% versus 23.8%) in protein content than the attached alga. However, attached Bryopsis is slightly lower in all the fiber components. It is worth noting that the drifts of loose Bryopsis can probably remain healthy and unattached indefinitely, so long as nutrients are sufficient, and currents weak enough, to prevent the drifts from being washed away (D. J. Russell, pers. commun., December 1983).

The mineral composition determined for the two different collections of Bryopsis is very similar (Table 11). The one prominent value for the nine minerals measured in these algae is the iron content of C. racemosa var. macrophysa (2,558 ppm). This level is many times higher than that of the uvifera variety (90 ppm) or either sample of Bryopsis (88 and 110 ppm). No firm explanation can be offered for these data. However, it is possible that macrophysa has a high requirement for iron, which therefore may be a limiting nutrient to growth. Iron pilings and pipes along the south shore of Johnston may supply this nutrient and allow the alga to proliferate as it does. This explanation is supported in part by data discussed in Russell and Carlson (1978) concerning shipwrecks and the concomitant vigorous growth of certain green algae.

Surveys to characterize and define the habitat limits for the different algae comprising the turtle foraging zone along the south shore resulted in the following findings. The occurrence of attached Bryopsis is confined almost entirely to the tops of coral heads that range from not more than 2 m beneath the surface, to those that are fully exposed at low tide. This environmental range appears to be a necessity for lush Bryopsis growth off the south shore. Only a limited number of coral heads fulfill the requirement. Many of the Bryopsis covered heads have growth 1-2 m down their slope, but thereafter the alga is sparse. A few small patches of attached Bryopsis were found on the sides of some heads as deep as 7.5 m.

The number of coral heads with Bryopsis was censused off the south shore at low tide from a boat on November 16. Between East Peninsula and the row of iron pilings (Fig. 1), 30 individual heads were counted, as well as a narrow broken ridge in shallow water parallel to shore. Between the iron pilings and the southwest side of West Peninsula, 31 heads were counted. From West Peninsula to the southwest corner of the island, 18 were counted. A total of only about 80 heads therefore occur in this narrow zone, and most (62) are between East and West Peninsulas. The greatest distance of any coral head from shore is about 600 m. Six of the heads that were believed to be representative of all the various sizes were selected and measured to determine vertical surface area where Bryopsis occurs. The heads were irregular and difficult to measure. Nevertheless, the areas ranged from approximately 9 to 127 m^2; the mean was 47 m^2. An "average" size coral head hosting Bryopsis is therefore only about 7 x 7 m. It was estimated that Bryopsis covered 80% of the surface area, the remainder being bare coral rock. This surface coverage could very well change with season. The distribution of Bryopsis off Johnston's south shore as portrayed in a map prepared by Applied Eco-Tech Services (1983: Fig. 24) greatly overrepresents the habitat area where this alga actually occurs.

As previously mentioned, there are coral heads to the northeast of East Peninsula where environmental conditions are conducive to Bryopsis growth and turtles were seen feeding. This area was not as thoroughly surveyed. There are probably not more than 15 coral heads there that host Bryopsis.

Turtles foraging on the tops of coral heads with Bryopsis are highly visible due to the shallow depth, and the contrasting color of the turtle's silty-brown shell against the green-black mat of Bryopsis. Because turtles are so apparent when foraging at these sites, it was possible to ascertain that some heads were being used more heavily than others. Cris Balubar also confirmed this point. For many heads, it is essential for the tide to be high enough for turtles to swim over the top to forage. At a few sites, this condition is never met. Two prominent coral heads off West Peninsula, are emergent much of the time, and even at high tide waves break with sufficient force to prevent turtles from feeding on top.

The growth of *Caulerpa* in the foraging habitat along Johnston's south shore is more difficult to characterize and define because, unlike *Bryopsis*, most of it cannot be seen from the surface. The extensive diving surveys with scuba devoted to examining habitat between the East and West Peninsulas helped to elucidate *Caulerpa* distribution. The *macrophysa* variety was far more abundant than *uvifera* or *serrulata*. The greatest *Caulerpa* coverage, approaching 100% on all hard substrate, occurred between the iron pilings and West Peninsula. Drifts of loose *Caulerpa* (again mostly *macrophysa*) covered nearly all of the silt bottom areas between the pinnacles and other hard substrate. There was a considerable decline in *Caulerpa* growth seaward from the outer iron pilings and the end of West Peninsula. At a point <100 m from the end of West Peninsula, in the area of net location 2 (Fig. 1), the growth of *Caulerpa* nearly disappears. Throughout this transition zone, the *Caulerpa* coverage declines first on the seaward sides of the underwater pinnacles. With the disappearance of *Caulerpa*, the hard substrate consists of bare rock, an increasing amount of live corals, and the *Bryopsis* previously described. A consistent salinity of 34‰ was recorded from nine water samples taken throughout the area, including one taken at the greatest bottom depth of 8 m. The seawater temperature ranged from 27.5° to 28.5°C.

The findings in this study relating to *Caulerpa* coverage between the iron pilings and West Peninsula are considerably different from those presented by Applied Eco-Tech Services (1983). Figure 23 in their report shows 80% to 100% coverage of *Caulerpa* on hard bottom substrate extending 200 m seaward of West Peninsula, twice the distance described in the present report. Possibly there was a radical seasonal change, since the survey by Applied Eco-Tech Services (1983) was done in June 1983, 5 months before the present study. Confirmation of this important point is needed.

The history of the marine environment off Johnston's south shore is virtually unknown due to the paucity of research conducted there. Sections of marine habitat have been filled in with the island's periodic expansion. When Cris Balubar arrived in 1962, he recalls many turtles being present off the south shore, along with clear water and "nice reefs." He does not remember the status of algal cover. Lee Gohr helped to lay the existing sewer outfall in 1964 and recalls seeing benthic algae, but not in the density that exists at present. None of the personnel interviewed was able to tell where the outfall existed before 1964.

The exact role of sewage discharge in facilitating, or possibly depressing, algal growth remains speculative. Aerial photographs of the island taken over the years may help to answer this question. It may be that nutrients from guano in the brackish-water lens of the island historically served as fertilizers for algae.

Epizoites and Abnormalities

Epizoic algal mats found mostly on the inguinal skin, plastron, and ventral surface of marginal scutes were sampled from five of the turtles captured. An analysis of this material revealed eight kinds of algae, roundworms, foraminifera, amphipods, and black "mites" (Table 12). One of the algal species (Pilina sp.) may possibly be a new record for the tropical Pacific. The red alga, Polysiphonia tsudana, was present on all five turtles, and is also common on Hawaiian green turtles. Acrochaetium, Sphacelaria, and Lygbya have also been recorded on green turtles in Hawaii, but for the latter two genera as different species. Urospora sp., found on three turtles, has never been reported from turtles in Hawaii. Amphipods found on two turtles and in the mouth and esophagus of another turtle are probably Hyachelia tortugae (Tables 7 and 8). This specialized crustacean, first described from the Galapagos Islands, has also been recorded in Hawaii and is known only from sea turtles.

There was a noticeable paucity of barnacles on the turtles captured. None of the common turtle barnacle, Chelonibia testudinaria, was present, nor was the burrowing barnacle, Stephanolepas muricata. Even more surprising was the near absence of the harmless skin barnacle, Platylepas hexastylos. Only a few were found on two turtles and some of these were falling off and appeared to be dying. Platylepas commonly occurs in large numbers on the skin of Hawaiian green turtles.

Small neoplastic growths 1-3 cm in diameter were found on two male turtles captured. Five growths were present on one and two on the other. The sites of these tumors included the trailing edge of front flippers, corner of the mouth, edge of the eye, inguinal region, and top of the head. Except for the latter location, growths are occasionally seen at these same places in Hawaiian and other green turtle populations. Some of the tumors documented elsewhere have been much larger, and far more numerous on individual turtles, than the ones seen at Johnston. However, Cris Balubar reported that about 10 years ago he did see a turtle "covered with white growths." The etiology of tumors on sea turtles is presently unknown. Relevant background material on the subject can be found in Harshbarger (1977), Balazs (1980c), Glazebrook et al. (1981), Jacobson (1981), and the references contained therein.

Counts made of the major scales along the trailing edge of the front flippers, to a point perpendicular to the claw scale, revealed that 2 (9.5%) of the 21 turtles varied from the standard 6 left-6 right count (Table 5).

The number of postocular scales (scales posterior of the orbits) varied from the standard 4 left-4 right count in 4 (19%) of the turtles (Table 5).

Four other abnormalities were noted among the turtles captured. The tail of an adult female was curled tightly under the edge of the carapace and appeared to be paralyzed. There was no scarring to suggest an injury.

One turtle made an unusual "whistling" sound when breathing. The cause could not be determined. Another had a small extra scute along the midline of the plastron between the humeral scutes, and another had a slightly depressed area to the carapace in the region of the 2d central scute and 1st-2d right lateral scutes. There were no signs of an external injury.

Predation and Injuries

Evidence of injuries likely resulting from shark attack was seen on 3 of the 21 turtles captured. The injury on an adult male was the most pronounced: half of its tail was amputated and it had extensive, but mostly healed, lacerations of the right hind flipper. Two turtles had several deep cuts in their carapace. Some of these wounds, which were also mostly healed, could be seen near the painted numbers. Five other turtles had minor pieces missing from hind flippers, but this is common in green turtles. None of the turtles in Cris Balubar's photos showed signs of shark attack or other obvious injuries. The few probable shark-inflicted injuries seen at Johnston may not necessarily have happened there, since the adult turtles must periodically migrate elsewhere for breeding purposes.

Sea turtles are known to be prey for large sharks, especially the tiger shark, _Galeocerdo_ _cuvier_. Captain Cameron was well aware of this food preference when he used turtles as bait to enhance his shark fishing at Johnston in 1892 (Farrell 1928). The graphic description by Benson (1953) of a shark swallowing a turtle whole at Johnston also attests to this fact. More recently, C. B. Cecrle, in litt. 1979 cited by Balazs (1982d), reported sharks feeding on a large turtle outside of the atoll.

Tiger sharks presently occur at the atoll, but they are not commonly seen nor frequently captured in recreational shark fishing. The most recent one caught was in August 1983 when a 4-m specimen was hooked in the ship channel at the western end of Sand Island. A 1-m whitetip reef shark, _Triaenodon_ _obseus_, was used as bait. The stomach was not cut open, so the natural prey items are unknown.

The gray reef shark, _Carcharhinus_ _amblyrhynchos_, often schools in abundance off the southwest corner of Johnston Island when kitchen garbage is dumped. Recreational fishermen fish for shark with baited hooks from shore here and at West and East Peninsulas. However, no reports were received of turtle parts ever being found in the stomach of gray reef sharks. Elsewhere this species is apparently not a regular predator of turtles, except possibly on hatchlings. One person interviewed stated that he had seen two turtles feeding on dead fish used as bait on a shark hook at West Peninsula.

Fishing for large tiger sharks used to be done with baited hooks set from markers along the main ship channel. This practice became prohibited, so personnel moored two large iron buoys 200-300 m offshore between West Peninsula and the southwest corner of the island. Both buoys are still present, but not often used for fishing since only small sharks (presumably gray reefs) have been caught there. During the diving surveys, only two sharks were seen, a gray reef at location M, and a whitetip at location L (Fig. 2). Large numbers of the former are said to enter the atoll for breeding purposes during the summer months.

The moray eel, Lycodontis javanicus (= Gymnothorax), occurs at Johnston Atoll where it is known to be an opportunistic predator of fish, octopus, and spiny lobsters (Brock 1972). This species is the largest moray eel in the Indo-Pacific; specimens seen at Johnston are estimated at up to 2.4 m long (Randall 1980). Lycodontis javanicus could conceivably prey on small immature green turtles, but there is no direct evidence showing this. However, a prey item as large (and unusual) as a 46.5 cm whitetip shark was found by Brock (1972) in the stomach of a 1.4 m moray eel. Eels live under ledges and in other coral recesses similar to where green turtles are typically believed to sleep. The eel's abundance and prey items have not been intensively studied along the south shore of Johnston Island. None was seen during any of the diving surveys. However, moray eels hide mostly in the reef during the daytime, and feed during twilight and at night.

Large groupers (Serranidae) occur at Johnston, but there is presently no evidence that they prey on turtles. In Hawaii, and elsewhere, whole immature turtles have occasionally been found in the stomachs of these fish. Benson (1953) describes the capture of a stunned "430 lb (195 kg) black sea bass" following an explosion to clear coral in the lagoon. The contents of the stomach were not mentioned. Sometime during 1970-71, a 27 kg grouper, Epinephelus sp., was caught at the southwest corner of Johnston Island near the garbage chute. The stomach was full of spiny lobsters (R. E. Brock, pers. commun., February 1984).

An unusual relatively minor injury was found on four of the turtles captured. This consisted of an ulcer on the dorsal neck surface over the supraoccipital bone of the skull. The exact cause is unknown, but could involve repeated abrasion against hard substrate, perhaps the roof of a coral recess where the turtles sleep.

Strandings

Information was obtained on strandings of four turtles. Three were described in interviews with resident personnel, and one by correspondence from the U.S. National Museum concerning the specimen mentioned in Amerson and Shelton (1976).

According to Cris Balubar, a large dead turtle "tangled in a Japanese fish net" washed up near East Peninsula several years ago. Also, at an unknown date a small turtle was found dead on the beach at Akau Island. No other information was available about these two incidents.

Phil Roseberry related that a few years ago he was told by Army personnel about a large dead turtle which washed in at Akau Island. He visited the site the next day, but the turtle was gone, presumably washed away by the next high tide.

Dr. Jack G. Frazier provided the following data on file for the specimen at the U.S. National Museum:

USNM 163581 (Catalogue entry)
Accession No. - 278016
Original No. - 11287
Name - Chelonia mydas/japonica
Locality - Sand Island, Johnston Atoll
Date collected - November 20, 1966
Received from - Smithsonian Institution Pacific Ocean Biological Survey Project
Collected by - --
When entered - September 14, 1967
Sex and No. of specimens - 1 head

Dr. Frazier also related that the head is approximately 10 cm wide and preserved in alcohol. It appears to have been collected fresh, and has a cut on the left side similar to what would result from a blow with a machete. This is the extent of information available. A 10-cm wide head would have come from a turtle about 75 cm SCL, hence of an immature size. Cris Balubar was unaware of this specimen, as were the other longtime residents interviewed. A probable scenario might be that a freshly dead turtle washed up at Sand Island from the adjacent ship channel. A short time later it was found by Smithsonian personnel, who used a machete or ax to sever the head for the museum's collection. One of these cuts may have accidently hit the side of the head. Other possible explanations might be that the gash resulted from a shark attack, or collision with a boat propeller. It seems unlikely that a live healthy turtle of this size would have been collected just for the head, unless the turtle was taken mainly for food or a trophy shell. By itself, and especially with no accompanying data, the head is of little taxonomic value, except to show the presence of Chelonia.

The U.S. National Museum's subspecies designation of japonica is the name sometimes applied to western Pacific green turtles. The type locality is Japan (Hirth 1971). Based on existing information, the use of this or any other trinomial for the Johnston population is not currently justified.

Basking

No evidence was found during the field study that green turtles bask ashore during the daytime, as they commonly do at Johnston's closest island neighbor, French Frigate Shoals in the Northwestern Hawaiian Islands (Whittow and Balazs 1982). Balazs (1978) indicated that the turtle collected at Sand Island in 1966 may have been basking (or nesting). However, this now seems unlikely in view of the information presented in the previous section.

Nitta (1982) stated that he received a report of turtles sometimes hauled out during the early morning on the coral-rubble and sand beach between the iron pilings and West Peninsula (Fig. 1). No turtles were found by Nitta (1982) when this site was visited at 0600 on July 9, 1982. Observers in the present study also surveyed the beach, which was 200 m long and accreted against the cement seawall that borders most of Johnston

Island. There were no marks in the beach suggestive of use by turtles. The site was visited on November 15 (2200), 16 (0500, and 2300) and 17 (0500), but no turtles were seen. Cris Balubar reported that the beach is unstable in that portions often wash away and return. He sometimes visits here early in the morning to look for baitfish, but has never seen a turtle ashore. Nevertheless, it is conceivable that turtles do occasionally come out at night to sleep along this shoreline when underwater sleeping sites become unacceptable due to storm surge or other factors. Such behavior is known at Necker Island and Pearl and Hermes Reef (Northwestern Hawaiian Islands), and on the Na Pali coast of Kauai, Hawaii.

An historic absence of basking by turtles at Johnston Atoll may have prompted the comment in 1859 by Brooke (MS.), quoted by Amerson and Shelton (1976), that "The reefs are covered with fish of various kinds. Mullet abound, but there are no turtles." Just 3 months earlier, in January 1859, Captain Brooke had visited French Frigate Shoals and Laysan Island, where he saw many turtles basking on the beach (Amerson 1971; Ely and Clapp 1973). These sights might easily have caused him to believe that land basking was common behavior for all sea turtles at remote Pacific islands. Seeing none along the shoreline at Johnston during his 2-day visit would naturally have come as a surprise, hence causing him to comment about no turtles being there. Since turtles were caught at Johnston 33 years later in 1892 by Captain Cameron (Farrell 1928), Brooke's (MS.) statement could not have been applicable to turtles in the water. It most likely meant that he expected to see turtles on the beach, and that no special search was made for them in the waters of the atoll. It should also be noted that when Captain Brooke arrived, 14 men were already living on Johnston Island, some since July 1858, building a wharf and railway for shipping guano (Amerson and Shelton 1976). Captain Cameron noted the abandoned remains of this facility in 1892 (Farrell 1928).

Reproduction

No historic records are known of turtles nesting at Johnston Atoll, although Amerson and Shelton (1976) speculate that perhaps they did in small numbers before habitation by man. Johnston Island was inhabited intermittently for guano removal starting in July 1858. Sand Island, however, seems to have remained uninhabited until the mid-1930's, when military construction began there.

The nesting season for green turtles in northern latitudes is from May through August. At French Frigate Shoals (lat. 23°45'N), the major nesting site for Hawaiian green turtles, the peak months are June and July. A similar season should exist at Johnston (lat. 16°45'N), if turtles nested there. The Tanager Expedition spent 10 days in July 1923 camped on uninhabited Johnston Island. According to Amerson and Shelton (1976), Wetmore (MS. a and b) "...recorded no turtles." However, from this statement it is unclear if Alexander Wetmore, leader of the expedition, actually noted an absence of turtles, or just made no mention of them in his field journal. The latter case applies for Wetmore (MS. b), but I have not seen Wetmore (MS. a). Nevertheless, while camped on Johnston Island, Wetmore (MS. B) tells of a nighttime walk along the beaches of "fine white coral sand." If turtles were seen coming ashore to nest in numbers, surely it would have been mentioned. This should also have been the case for any extensive nesting excavations seen in the vegetation zone during numerous daytime surveys. However, it is conjecture if the same would also apply for Sand Island. There were no overnight camps there, and only two daytime visits were made.

It should be noted that the Tanager Expedition had just come from French Frigate Shoals and other Northwestern Hawaiian Islands, where journal notes were in fact made about turtles basking, nesting, and being recently exploited (Amerson 1971). The expedition constituted the first discovery by scientific personnel of sea turtles actually basking. Consequently, most of the interest relating to turtles was focused on this behavioral aspect (Mellen 1925; Wetmore 1925).

The question of whether or not turtles nested at Sand or Johnston Island when the Tanager Expedition visited in 1923 can probably be answered conclusively from aerial photographs. A small seaplane made the first photographic flights over the atoll during the expedition on July 12 and 19 (Wetmore MS. b). These and other U.S. Navy aerial photos taken until the late 1930's should be of sufficient resolution to show nesting excavations, if such sites existed. The original photos are apparently on file in the U.S. National Archives (Amerson and Shelton 1976).

During his residency at Johnston Island since 1962, Cris Balubar only knows of one instance of a possible nesting, but couldn't recall the year. Turtle tracks and digging were seen at Sand Island, but there was no confirmation that eggs were laid. Cris Balubar also stated that he had never seen eggs inside turtles he had caught and cleaned. Upon further discussion, it was determined that only ova of a large and nearly mature size would have been noticed and remembered by him.

Several people interviewed, including Cris Balubar, said that they had seen turtles locked together copulating, sometimes for extended periods. Cris Balubar felt that this mating activity was more prevalent during September through November. Francisco Aguinaldo and Ed Mattson saw a copulating pair in July 1983 at the shoreline of the sand beach by the iron pilings. The turtles swam off quickly when approached. Previous occurrences of this sort may have been partly responsible for the report received by Nitta (1982) of turtles hauling out on this beach. Present accounts of turtles copulating at Johnston are supported by the fact that, in 1892, Captain Cameron tethered a few receptive females to attract and catch males intent on mating (Farrell 1928). The contradiction here is that, for the most part, green turtles are thought to mate only in waters adjacent to their nesting beach.

The lesions typically present on males and females following copulation were not seen on any of the turtles captured in this present study.

A survey of Sand Island's shoreline identified four sand beaches, all located at the eastern end which comprised the original portion of the island before enlargement. Each of these natural beaches offers access to the elevated interior where the soil is suitable for nesting. With the exception of one beach where there is a bright electrical light, Sand Island presently seems to be appropriate habitat for nesting, if turtles wanted to nest there. Even the beach by the iron pilings on Johnston Island has an elevated area of fine sand where nesting might successfully take place. In contrast, the man-made islands of Akau and Hikina are unsuitable, since the shorelines consist only of cement seawalls and coarse coral rubble, and the interiors are compacted aggregate from dredging.

Migrations

Since there presently is no nesting at Johnston Atoll, and possibly never was, the turtles must be periodically migrating elsewhere to reproduce. This would be consistent with the pattern found in most other green turtle populations, where round trip migrations take place between resident foraging areas and distant breeding grounds. Migrations of this nature are known to be made, even when what may appear to be acceptable nesting beaches are close by. Though not conclusively proven, the turtles are most likely returning to breed at their natal beaches.

A logical place where Johnston's turtles might go to nest would be French Frigate Shoals. This site is only 830 km to the north, and comprises the major rookery for green turtles migrating from islands throughout a 2,200 km expanse of the Hawaiian Archipelago. However, there are no tag recoveries to support the hypothesis of French Frigate Shoals actually being the breeding site for Johnston's turtles. Ample opportunities have existed for such a migratory pattern to be demonstrated. Over the past 20 years, more than 1,600 adults have been tagged at French Frigate Shoals, and about 200 others tagged elsewhere in the Northwestern Hawaiian Islands. None of these tagged turtles has been recovered in the Johnston population, neither in the present study, nor when turtle fishing was allowed at the atoll. Cris Balubar estimates he caught 60 turtles between 1967 and 1976, but found no tags. These same years were some of the most intensive for tagging turtles at French Frigate Shoals. Interestingly, during the years 1966-72, 860 Hawaiian monk seals, Monachus schauinslandi, were also tagged in the Northwestern Hawaiian Islands. Three of these have subsequently been reported at Johnston; one came from French Frigate Shoals, and two from Laysan Island (Schreiber and Kridler 1969; Johnson and Kridler 1983). Monk seals were apparently a conspicuous component of Johnston's fauna when Captain Cameron visited there in 1892 (Farrell 1928). In this century, however, very few seals are known to have migrated outside the Hawaiian Archipelago, and then only to Johnston Atoll. A migratory link between Johnston and French Frigate Shoals also exists for seabirds. Of 733 inter-island tag recoveries, 32% involved French Frigate Shoals (Amerson and Shelton 1976).

The isolated location of Johnston limits the number of other sites the resident turtles might go to nest. The Line Islands, starting with Kingman Reef 1,575 km to the southwest, is the next closest area to Johnston after French Frigate Shoals and the other Northwestern Hawaiian Islands. A low level of green turtle nesting occurs at the inhabited atolls of Fanning and Christmas in this island group. But none is known to occur at Kingman, nor the nearby atoll of Palmyra.

The closest island to the west of Johnston is uninhabited Bikar in the northern Marshall Islands. Bikar is located 2,220 km away and is considered a prominent nesting site for green turtles (Pritchard 1982). No tagging has been conducted at Bikar, so the resident foraging grounds for turtles nesting there are unknown. Presumably they include many of the Marshall Islands. Bikar is a traditional wildlife reserve owned by chiefs of a Marshallese clan who periodically visit to gather turtles, seabirds, and their eggs (Tobin 1952).

Canton and other islands of the Phoenix group are situated almost directly south of Johnston, below the Equator, at a closest distance of 2,160 km. Green turtles have been found to nest here, but again the areas where they migrate from are currently unknown (Balazs 1975).

The limited amount of tagging done in the Pacific has uncovered some impressive long distance migrations by turtles, each encompassing the boundaries of several island nations (Balazs 1982c). Turtles tagged at Johnston in the present study may very well yield similar results, and eventually pinpoint the nesting site.

From interviews, it was learned that three turtles had been marked at Johnston before the tagging done in this study. In 1971, Cris Balubar tagged a turtle (on the dorsal surface of a front flipper) with an aluminum plate embossed with his name, location (Johnston), weight of the turtle (130 lb (59.1 kg)), and date of release. The day and month could not be recalled. He also caught another turtle sometime in 1971 described as being "large and ugly," but apparently not diseased or injured. The carapace of this one was painted completely black before it was released. A second turtle was also marked with paint. This one weighed only about 14 kg and was hand captured by someone else close to shore at Hikina Island. The words "Happy New Year January 1981" were stenciled on the carapace with fluorescent paint. No recoveries have been reported for these three turtles.

Utilization

It is not possible to quantify the number of turtles taken at Johnston over the years, except for the estimate of 60 given by Cris Balubar for 1967-76. An estimate of 12-15 turtles harvested per year by "a long time resident" appears in Amerson and Shelton (1976).

All turtles caught at the atoll since military occupation in the 1930's can be assumed to have been taken for sport, trophy shells, and as a seafood delicacy along with fish and lobster. There is no evidence of commercial harvest during this period, although some shells were probably sold privately. In 1976 the refuge manager for the U.S. Fish and Wildlife Service (Palmer Sekora) prohibited all taking of turtles at Johnston. This measure was instituted to achieve consistency with the already protected status of sea turtles at other National Wildlife Refuges in the United States.

Cris Balubar's case history of turtle fishing is worth describing, since he is well known locally for this skill. He appears to be the only person over the past 22 years who regularly targeted turtles with a specific fishing technique. This viewpoint could, however, be biased due to Cris Balubar's long residency, and since he is still there to be interviewed. Other personnel fishing just for turtles may have come and gone over the years, leaving no verbal record of their activities. Turtle catching by others was probably only on an opportunistic basis while diving and spearfishing. For instance, some years ago Lee Gohr caught a 59-kg turtle while recreational diving between Sand and North Islands. Also, since turtle fishing has been illegal since 1976, it is unlikely any information would be volunteered about turtles taken thereafter. A secondhand report, believed to be reliable, was received that occasionally turtles are still taken for food when they are accidentally encountered by divers in the north of the atoll. In these instances, it was reported the divers discard the shell and flippers before returning to Johnston Island.

Cris Balubar's turtle fishing started in 1967 when he was asked to catch a turtle for one of the island's military officers. As it is now, most turtles were found along the south shore. West Peninsula was generally off limits for recreational purposes at that time. However, special permission for fishing was granted in this case. The technique successfully employed involved a fiber glass pole with a spinner reel and treble hook to cast out and snag the turtle while it was feeding. A lengthy period would then often be needed to reel it in. The turtle incurred very little physical injury during capture, since it was usually hooked only in a flipper. This fishing method is a modification of one sometimes used for turtles in Hawaii (Balazs 1980c). Cris Balubar subsequently caught turtles in this manner from a small boat off the south shore, as well as from the seawall. He estimates that 45 of the 60 turtles taken were by boat. According to Balubar, Johnston turtles taste much better than Hawaiian turtles. This difference could be due to the algal food sources utilized. A recent article in Hawaii Fishing News describes his snagging technique used to land a large yellowfin tuna from the seawall at Johnston (Balubar 1982).

The only firm evidence of turtles being exploited at Johnston before military settlement is Captain Cameron's mention of their use in 1892 for shark bait and food (Farrell 1928). Turtles, along with seals, were a preferred bait for shark fishing at that time. It is reasonable to assume that other commercial fishing expeditions stopping there would also have taken turtles, if they could be found. In 1918 an attempt was made to establish a fishing station at Johnston, but dissatisfied workers quickly terminated the plan. During the 1920's, at least two commercial fishing vessels visited the atoll. One was the Lanikai, a vessel known to take turtles from Pearl and Hermes Reef for markets in Honolulu (Thurston 1928; Amerson and Shelton 1976; Balazs 1980c). Brock et al. (1965) imply that at least one fishing boat from Honolulu regularly visited Johnston before World War II.

Guano mining outposts on remote Pacific islands, like the one started at Johnston in 1858, regularly used whatever marine resources were available for fresh food. Turtles were among those items eaten by guano diggers on Laysan Island. Presumably turtles were also eaten at other guano islands where they were present. Turtles were also eaten at the intermittent camps set up illegally by plume hunters in the Northwestern Hawaiian Islands. The remains of such a camp were found at Johnston in 1923 (Wetmore MS. b).

Environmental Perturbations

A number of man-made perturbations have historically taken place at Johnston that could have adversely affected turtles. Some of these impacts, like blasting to remove coral, almost certainly caused direct mortality. Others have possibly been more subtle, thus making them difficult to detect (Whittle et al. 1977). The highly modified environment at Johnston, and the various uncommon activities periodically conducted there, warrant the consideration of these perturbations. It is beyond the scope of this paper to give an in-depth evaluation and analyses of these factors. However, the information contained herein should provide some direction for possible future research of turtles at Johnston Atoll.

Initial blasting and dredging to clear coral and increase the size of Johnston and Sand Islands happened from 1939 to 1942. Woodbury (1946) describes the difficulties experienced in breaking up the coral, and the extraordinary amount of dynamiting required. Johnston Island was expanded from its original 19 ha to 85 ha, and 4-ha Sand Island was doubled in size. Major construction projects to further enlarge Johnston Island were completed in 1958 and 1964, resulting in the present land area of 253 ha. The man-made islands of Akau (10 ha) and Hikina (7 ha), with channels leading to them, were also finished in 1964 (U.S. Army Corps of Engineers 1983). The concussions from underwater explosions during these various projects would have stunned any turtle in the vicinity causing injury and death from direct impact or drowning. Such blasting, and the resulting dead fish, would also be an attractant to large sharks that could, in turn, easily have preyed on stunned turtles. The likelihood that this actually happened is supported by Benson's (1953) description of "...numerous huge sharks" being present during dynamiting, and one of them seen "...swallowing a sea turtle whole." Underwater explosions have also been set off occasionally in recent years. Moses Caballero mentioned the destruction of a live bomb found in the turning basin of the ship channel. It should be noted that some blasting also occurred in the lagoon waters of Johnston long before military activities. During Captain Cameron's 1892 visit, at least one marine harvest was made by driving fish close to shore and setting off "dynamite cartridges" (Farrell 1928: p. 406).

Several hydrogen bombs were successfully detonated at high altitude over Johnston in 1958 and 1962. Amerson and Shelton (1976) stated the following with respect to one of the environmental impacts:

> "During these nuclear tests, an elaborate water sprinkler system was installed on the original portion of Sand Island to protect the birds living there. In addition, other protective devices were used, including smoke pots placed upwind as a shade screen and aerial flares to divert the birds' attention from the flash of the blast itself."

Since the flash (and heat?) from these explosions was so intense at ground level, eye damage could presumably have resulted to any turtles on or near the surface at the time of detonation.

During 1962, three of the missiles carrying nuclear devices malfunctioned, exploded, and spread particles of radioactive material over the atoll and surrounding Pacific Ocean. One of these blasts was on the launch pad, significantly affecting a portion of Johnston Island (Anonymous 1962a, 1962b, 1962c). Decontamination efforts have been periodically carried out, including removal and dumping of debris and surface soil over deep water outside the atoll. As a result, some contaminated soil entered the nearshore waters of the island and certain areas of the island continue to be "off limits." The surface runoff of rainfall undoubtedly transports additional particles into the nearshore waters. The soil at the western end of Sand Island is also still contaminated (U.S. Army Corps of Engineers 1983). Benthic algae, including types which exist in the turtle foraging habitat along the south shore, concentrate certain radionuclides at rates higher than other plants and animals (Hines 1962: p. 145-151; Whittle et al. 1977). Hillestad et al. (1974) reported very low levels of gamma emitters in tissue from loggerhead turtles, Caretta caretta, in Georgia and South Carolina. The levels present in turtles from a contaminated area are apparently unknown.

During the early 1970's, various chemical weapons and herbicides were stored on Johnston Island. Also, canisters of dioxin were flown to the atoll in 1976 (Benson 1976). The herbicide was safely incinerated at sea in 1977 using a ship built for such purposes (Nelson 1977). However, leakage from these drums resulted in Herbicide Orange and dioxin contamination of soil at the northwest corner of the island. In 1973, various water, sediment, and marine biological samples were tested for dioxin and Herbicide Orange. A muscle and liver specimen from a green turtle of unknown size, taken between East and West Peninsulas, were included. A sample of Bryopsis, but not Caulerpa, from the same area was also analyzed. None of these four samples from 1973 (presumably measured on a dry matter basis) was found to have detectable levels of dioxin or Herbicide Orange (U.S. Army Corps of Engineers 1983: footnote in Table III-6, Appendix L).

Some leakage of nerve gas from deteriorating munitions containers has been reported (Borg 1982). As noted in a previous section, wash water from the decontamination procedure is discharged through the sewer outfall directly into the turtle foraging habitat. Storm drains may also receive some of this effluent.

A considerable amount of man-made debris was seen on the ocean bottom during diving surveys at locations G and U (Fig. 2). These were the only two offshore (>14 m) sites surveyed, so discarded items may exist over a much broader area off Johnston Island's south shore. The material seen consisted of 55-gal drums, a trailer, a Mike boat, and pieces of iron reinforcement bar. The drums were heavily rusted, but some appeared intact. The contents, if any, could not be determined through interviews with resident personnel.

Heavy metals are known to be discharged from desalination plants as the result of internal corrosion. Two types of discharge have been reported: one emitted when the plant is operating normally, the other produced during periodic cleaning and maintenance cycles (Chesher 1975).

High levels of copper are present in the normal effluent, and this element is believed to be the most toxic to marine organisms. When desalination plants shut down for maintenance, corroded copper-nickel surfaces dry and oxidize. With resumption of operation, copper contamination is 2-3 times higher than normal for a few hours. Higher levels of nickel and iron are also released. The discharge during this period is turbid and black (Chesher 1975). Few studies have attempted to measure heavy metal content in sea turtles and their eggs (Hillestad et al. 1974; Stoneburner et al. 1980; Witkowski and Frazier 1982). Furthermore, as emphasized by Witkowski and Frazier (1982) and Coston-Clements and Hoss (1983), it is difficult to determine the significance of such findings because little is known about baseline levels and physiological effects. Based on reports of copper levels discharged from a desalination plant (Chesher 1975), the facility at Johnston probably produces at present 1.3-2.6 kg of copper effluent per day under normal operation. Effluent from the plant apparently also serves to enrich, by some undetermined process, the existing radionuclide contamination in nearshore waters, thereby producing a localized "hot spot" (U.S. Army Corps of Engineers 1983: Appendix L, p. 5-6). Whether or not cooling water from other facilities besides desalination would do the same is unknown.

Petroleum spills can adversely affect turtles by external fouling, ingestion, and interference with olfactory perception and food supply (Coston-Clements and Hoss 1983). During the field study at Johnston, dried petroleum matter was found adhering to the seawall at the east corner of West Peninsula. It had likely gathered and washed up there from the funneling effect of prevailing winds and currents. The age of the material, and the length of time required for it to accumulate, could not be determined. Turtle foraging habitat around West Peninsula, and along much of the south shore, appears to be vulnerable to petroleum contamination due to its windage and proximity to the ship channel.

Artificial illumination on beaches is known to discourage adult turtles from nesting and disorient hatchlings crawling to the sea (Coston-Clements and Hoss 1983). However, almost no information exists on the effects of coastal lights on turtles foraging or sleeping at night in nearshore habitat. Nocturnal feeding is common behavior for green turtles in Hawaii (Balazs 1980c). However, at Johnston the catch rates from nets, and direct observations made from shore, suggest that foraging is mostly, if not entirely, during the daytime. Between West Peninsula and the island's southwest corner there are nine white lights of medium intensity set on posts 75-100 m inland. In addition, 23 dim yellow lights are located on the chemical storage bunkers facing the shoreline. None of these lights directly illuminate the nearshore waters, although they are clearly visible from offshore. At present, there are no lights on posts anywhere near the shoreline of West Peninsula itself.

Cholinesterase

Very low concentrations of organophosphorus compounds inhibit the activity of cholinesterase, an enzyme responsible for important physiological processes in the nervous system. Cholinesterase also occurs in serum and red blood cells. The inhibitory effect of organophosphorus compounds is the basis for their use as insecticides and certain chemical weapons. Cholinesterase inhibition can also be used to biochemically detect organophosphorus compounds in the environment or in an organism (Namba 1971; Lundin 1975).

At Johnston Island, red blood cell cholinesterase is measured in humans by the 17-Minute Manual Method. According to information supplied by Lucille Bodnar, who routinely performs this analysis at Johnston, the method is based on the principle that cholinesterase hydrolyzes acetylcholine bromide with the production of acetic acid. The change in pH is measured in a barbital-phosphate buffer when red blood cells are mixed with a known excess of acetylcholine bromide and allowed to hemolyze. The results are expressed in terms of the decrease in pH units during the 17-minute reaction period. The normal range for humans is 0.63-0.89 pH/h.

Cholinesterase values, using a 0.2 ml aliquot of red blood cells, were determined by this method for six adult and three immature turtles (Table 13). The validity of these results is unknown, since the analysis is designed for human blood. The method may be unsuitable for turtle blood due to the capacity of the buffer, size of aliquot used, or other factors. Verification is needed. In addition, the normal range of decrease in pH units for the green turtle is currently unknown. Given these analytical uncertainties and the small numbers sampled, Table 13 shows that cholinesterase for the nine turtles ranged from 0.13 to 0.34 pH/h. It is worth noting that the mean value for the three adult males (0.27 pH/h) was almost double the mean of the three adult females (0.14 pH/h). Also, the two immature females measured had levels similar to the adult males. Two of the nine turtles sampled were caught at net location 7, downwind of the sewer outfall. There is no indication from these few data that differences exist between sampling locations.

RECOMMENDATIONS

Management Measures

The information contained in this paper provides a basis for offering recommendations of management measures to help ensure the conservation of turtles at Johnston Atoll. These actions are:

1. A specific management zone for marine turtles should be established. The area should encompass marine habitat extending seaward for about 1 km along the entire south shore of Johnston Island, as well as a contiguous band extending about 1.5 km to the northeast of the main ship channel. The purpose of this zone would be to give special attention to the turtles concentrated there and the habitat upon which they depend. An appropriate and distinct mechanism would then exist to soundly manage the area on a continuing basis. The designation would be particularly helpful for identifying and evaluating any potential impacts to turtles and habitat that might arise in the future. The zone would be fully consistent with the environmental goals of the JACADS project and, in fact, the project would likely benefit from the special management attention given to the turtles.

2. A management action needed at present is the curtailment of any recreational boats transiting or anchoring in the area described above. The rapid diving response when turtles are approached by boats indicates that normal foraging behavior is easily disrupted. This may be the result of previous human harassment, including fishing efforts to hook them and regular encounters with small boats.

3. A formal system should be implemented to deal with any future strandings of dead or live turtles. Rapid reporting, and the appropriate immediate response by interested parties, is absolutely essential for these cases. Valuable specimens and data can be acquired in this manner; for example, bones for age determination, whole stomach contents, tissue samples, and a determination of the cause of death or debilitation. The presence of a tag further increases the worth of the specimen. The system should also include turtles or their parts found in the stomach of sharks and other predators.

4. An informative, interesting, and inexpensive brochure, preferably with illustrative photographs, should be prepared telling about the turtles at Johnston, where they principally occur, and their protected status under the U.S. Endangered Species Act. The brochure should be specific for turtles, and not done in descriptive combination with other wildlife or marine resources of the atoll. The brochure should be distributed at the air terminal to each new person upon arrival.

5. A formal response plan should be prepared describing the actions to be taken in the event of a petroleum spill involving the area described for a turtle management zone. Special attention should be given to sites around West Peninsula where spillage may concentrate.

6. A plan to assess the effects, if any, of newly installed lights on the foraging behavior and other use patterns of green turtles off West Peninsula should be developed. This should encompass the temporary lights needed during active construction of JACADS, as well as permanent security lights planned for the completed facility.

Future Research Activities

The successful long-term management of these turtles is, to a large extent, dependent upon a certain amount of future research being accomplished. Research on turtles at Johnston has long been neglected. However, from this present assessment it is apparent that they constitute an ecologically important, scientifically challenging, and historically interesting part of the atoll's fauna. In addition, Johnston's turtles are most likely used for food by native people somewhere in the Pacific islands, since it is doubtful they nest at French Frigate Shoals where full protection would be afforded. A major research and management goal should be to determine the international migrations of these turtles, including their ultimate destination and island areas of transit where fishing may occur. The only way to achieve this objective at an early date is to capture and tag more turtles at Johnston. The relatively high proportion of adults and females found in the population will be an advantage to understanding the movement patterns, since it will increase the probability of long-distance recoveries.

The following recommendations relate to research that should be accomplished to facilitate a better understanding of the biology of this turtle population. The information developed in these studies will also serve as a basis to formulate future management measures for Johnston's turtles. While this research is clearly needed, it is outside the scope of this paper to indicate specific agency responsibility or priorities for support of this work.

1. A standard monitoring program should be established to assess and tag turtles periodically in a manner similar to the present study. This action will be particularly important during the active construction phase of the JACADS project. During this period, three 10-day study visits per year are deemed necessary. Thereafter, one or two visits per year would be sufficient.

2. Diving surveys with scuba should be made between West Peninsula and the southwest corner of Johnston Island to search for turtle sleeping areas. To accomplish the dives safely, formal arrangements must be made to delay, for 2 h daily, the interval pumping of sewage from the outfall over a 3-4 day period. This appears feasible at present during midmorning when water usage is normally low. However, it must be done before the large increase in personnel scheduled for the JACADS project.

3. The blood analysis used in the present study to measure cholinesterase should be evaluated and, if needed, modified to obtain accurate measurements. Routine testing of cholinesterase in turtles should be conducted as part of the periodic monitoring suggested in recommendation 1 above. The normal range for green turtles should be determined from blood sampling currently underway in Hawaii.

4. The enrichment of radionuclide contamination by effluent from the desalination plant should be elucidated. The possible role of heat and heavy metals in this process should be examined to ascertain if discharge water planned for JACADS will produce similar enrichment, which in turn may be transferred to turtles through algal food sources.

5. Aerial photographs taken over Johnston Atoll should be located and examined to determine the past distribution of benthic algae and if nesting occurred during the period before large scale inhabitation by man.

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LITERATURE CITED

Amerson, A. B., Jr. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. Atoll Res. Bull. 150:1-383.

Amerson, A. B., Jr., and P. C. Shelton. 1976. The natural history of Johnston Atoll, central Pacific Ocean. Atoll Res. Bull. 192:1-479.

Anonymous. 1962a. Warhead detonation is averted. The Honolulu Advertiser, July 27, 1962.

1962b. Site repairs may take up to eight weeks. Honolulu Star-Bulletin, July 31, 1962, p. 1.

Anonymous. 1962c. Destroys Johnston N-shot. The Honolulu Advertiser, Oct. 16, 1962, p. 1-2.

Applied Eco-Tech Services, Inc. 1983. Johnston Atoll water quality and current study - a final report. Report submitted to U.S. Army Engineer District, Honolulu, 24 Aug. 1983, 100 p.

Balazs, G. H. 1975. Marine turtles in the Phoenix Islands. Atoll Res. Bull. 184:1-7.

1976. Green turtle migrations in the Hawaiian Archipelago. Biol. Conserv. 9:125-140.

1978. Terrestrial critical habitat for sea turtles under United States jurisdiction in the Pacific region. 'Elepaio 39(4):37-41.

1980a. Field methods for sampling the dietary components of green turtles, *Chelonia mydas*. Herpetol. Rev. 11(1):5-6.

1980b. A review of basic biological data on the green turtle in the Northwestern Hawaiian Islands. *In* R. W. Grigg and R. T. Pfund (editors), Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii, p. 42-54. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-4.

1980c. Synopsis of biological data on the green turtle in the Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-7, 141 p.

1982a. Factors affecting the retention of metal tags on sea turtles. Mar. Turtle Newsl. 20:11-14.

1982b. Growth rates of immature green turtles in the Hawaiian Archipelago. *In* K. A. Bjorndal (editor), Biology and conservation of sea turtles, p. 117-125. Smithson. Inst. Press, Wash., D.C.

1982c. Sea turtles: A shared resource of the Pacific islands. South Pac. Comm. Fish. Newsl. 23:22-24.

1982d. Status of sea turtles in the central Pacific Ocean. *In* K. A. Bjorndal (editor), Biology and conservation of sea turtles, p. 243-252. Smithson. Inst. Press, Wash., D.C.

1983. Recovery records of adult green turtles observed or originally tagged at French Frigate Shoals, Northwestern Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-36, 42 p.

Balubar, C. 1982. Biggest fish story--mail buoy. Hawaii Fish. News 7(10):8.

Benson, B. 1953. Johnston Island--it's not exactly paradise. Honolulu Star-Bulletin, Nov. 8, 1953, magazine section, p. 15.

1976. Air Force flies deadly dioxin canisters to Johnston Atoll. The Honolulu Advertiser, Dec. 9, 1976, A:14.

Bentley, T. B., and A. Dunbar-Cooper. 1980. A blood sampling technique for sea turtles. Final report for contract No. NA-80-GE-A-00082, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 14 p.

Borg, J. 1982. Nerve gas leaks seen under control. The Honolulu Advertiser, Nov. 4, 1982, A:5.

Brock, R. E. 1972. A contribution to the biology of Gymnothorax javanicus (Bleeker). M.S. Thesis, Univ. Hawaii, 121 p.

Brock, V. E., R. S. Jones, and P. Helfrich. 1965. An ecological reconnaissance of Johnston Island and the effects of dredging. Univ. Hawaii, Hawaii Mar. Lab., Tech. Rep. 5, 90 p.

Brock, V. E., W. Van Henkelem, and P. Helfrich. 1966. An ecological reconnaissance of Johnston Island and the effects of dredging. Second Annual Report. Univ. Hawaii, Hawaii Mar. Lab., Tech. Rep. 11, 56 p.

Brooke, J. M. MS. Journal of the Fenimore Cooper for 1859. [Unpublished manuscr.] G. M. Brooke, Jr., Lexington, Va.

Buggeln, R. G., and R. T. Tsuda. 1966. A preliminary marine algal flora from selected habitats on Johnston Atoll. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 9, 29 p.

1969. A record of benthic marine algae from Johnston Atoll. Atoll Res. Bull. 120:1-20.

Carr, A. 1972. Great reptiles, great enigmas. Audubon 74(2):24-35.

Chesher, R. H. 1975. Biological impact of a large-scale desalination plant at Key West, Florida. In E. J. Ferguson Wood and R. E. Johannes (editors), Tropical marine pollution, p. 99-153. Elsevier Oceanogr. Ser. 12.

Coston-Clements, L., and D. E. Hoss. 1983. Synopsis of data on the impact of habitat alteration on sea turtles around the southeastern United States. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-SEFC-117, 57 p.

Dawes, C. J., and R. H. Goddard. 1978. Chemical composition of the wound plug and entire plants for species of the coenocytic green alga, Caulerpa. J. Exp. Mar. Biol. Ecol. 35:259-263.

Ely, C. A., and R. B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Res. Bull. 171:1-361.

Farrell, A. (transcriber). 1928. John Cameron's odyssey. The MacMillan Co., 461 p.

Glazebrook, J. S., R. S. F. Campbell, and D. Blair. 1981. Pathological changes associated with cardiovascular trematodes (Digenea: Spirorchidae) in a green sea turtle *Chelonia mydas* (L). J. Comp. Pathol. 91:361-368.

Harshbarger, J. C. 1977. Role of the registry of tumors in lower animals in the study of environmental carcinogenesis in aquatic animals. *In* H. F. Kraybill, C. J. Dawe, J. C. Harshbarger, and R. J. Tardiff (editors), Aquatic pollutants and biologic effects with emphasis on neoplasia, p. 280-289. New York Acad. Sci., N.Y.

Hillestad, H. O., R. J. Reimold, R. R. Stickney, H. L. Windom, and J. H. Jenkins. 1974. Pesticides, heavy metals and radionuclide uptake in loggerhead sea turtles from South Carolina and Georgia. Herpetol. Rev. 5(3):75.

Hines, N. O. 1962. Proving ground. Univ. Washington Press, Seattle, 366 p.

Hirth, H. F. 1971. Synopsis of biological data on the green turtle *Chelonia mydas* (Linnaeus) 1758). FAO Fish. Synop. 85, 1:1-8:19.

Ireland, L. C. 1979a. Homing behavior of immature green turtles (*Chelonia mydas*). Am. Zool. 19:952.

1979b. Homing behavior of juvenile green turtles, *Chelonia mydas*. *In* C. J. Amlaner, Jr., and D. W. MacDonald (editors), A handbook of biotelemetry and radio tracking, p. 761-764. Pergamon Press, Oxford.

Jacobson, E. R. 1981. Virus associated neoplasms of reptiles. *In* C. J. Dawe, J. C. Harshbarger, S. Kondo, T. Sugimura, and S. Takayama (editors), Phyletic approaches to cancer, p. 53-58. Jpn. Sci. Soc. Press, Tokyo.

Johnson, A. M., and E. Kridler. 1983. Interisland movement of Hawaiian monk seals. 'Elepaio 44(5):43-46.

Ludwig, G. M. 1982. Trip report: Johnston Atoll, September 12-17, 1981. U.S. Fish and Wildlife Service, Honolulu, 20 p.

Ludwig, G. M., S. Fefer, J. Maragos, and E. Nitta. 1982. JACADS project environmental survey at Johnston Atoll NWR July 8-11, 1982. Trip report. U.S. Fish Wildl. Serv., Honolulu, 21 p.

Lundin, S. J. 1975. The inhibition of cholinesterase activity by organophosphorus compounds as a means of an inspection procedure. *In* The problem of chemical and biological warfare. Vol. VI. Technical aspects of early warning and verification, p. 177-183. Humanities Press, N.Y.

Meinesz, A. J. Jaubert, and M. Denizot. 1981. Distribution of the algae belonging to the genus Caulerpa in French Polynesia (atoll of Takapoto and island of Moorea). Proceedings of the Fourth International Coral Reef Symposium, Manila 2:431-437.

Mellen, I. M. 1925. Marine turtles sleep on Hawaiian sands. N.Y. Zool. Soc., Bull. 28:160-161.

Menzies, R. A., L. Kochinsky, J. M. Kerrigan. 1983. Techniques for muscle biopsy and blood sampling from sea turtles. Poster session presented at the Western Atlantic Turtle Symposium, July 17-22, 1983, San Jose, Costa Rica, 2 p.

Namba, T. 1971. Cholinesterase inhibition by organophosphorus compounds and its clinical effects. Bull. WHO 44:289-307.

Nelson, L. 1977. Herbicide burning to end this week. Honolulu Star-Bulletin, July 27, 1977, C:4.

Nitta, E. T. 1982. Johnston Atoll field trip report, July 1982. Southwest Region, Western Pacific Program Office, Natl. Mar. Fish. Serv., NOAA, Honolulu, 6 p.

Owens, D. W., and G. J. Ruiz. 1980. New methods of obtaining blood and cerebrospiral fluid (from marine turtles. Herpetologica 36:17-20.

Paul, V. J. 1983. Strategies of chemical defense in tropical marine algae of the order Caulerpales (Chlorophyta). (Abstract.) 64th Annual Meeting of the Western Society of Naturalists, Burnaby, British Columbia.

Paul, V. J., and W. Fenical. 1982. Toxic feeding deterrents from the tropical marine alga Caulerpa bikinensis (Chlorophyta). Tetrahedron Lett. 23, 48:5017-5020.

Pritchard, P. C. H. 1982. Marine turtles of the South Pacific. In K. A. Bjorndal (editor), Biology and conservation of sea turtles, p. 253-262. Smithson. Inst. Press, Wash., D.C.

Rainey, W. E. 1981. Guide to sea turtle visceral anatomy. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SEFC-82, 82 p.

Randall, J. E. 1980. A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes. Fish. Bull., U.S. 78:201-249.

Russell, D. J., and B. A. Carlson. 1978. Edible-oil pollution on Fanning Island. Pac. Sci. 32:1-15.

Schreiber, R. W., and E. Kridler. 1969. Occurrence of an Hawaiian monk seal (Monachus schauinslandi) on Johnston Atoll, Pacific Ocean. J. Mammal. 50:841-842.

Stoneburner, D. L., M. N. Nicora, and E. R. Blood. 1980. Heavy metals in loggerhead sea turtle eggs (Caretta caretta). Evidence to support the hypothesis that demes exist in the western Atlantic population. J. Herpetol. 14:171-175.

Thurston, L. A. 1928. Features of Johnston Island. The Honolulu Advertiser, Aug. 5, 1928, p. 4, 11.

Tobin, J. E. 1952. Land tenure in the Marshall Islands. Atoll Res. Bull. 11:1-36.

U.S. Army Corps of Engineers. 1983. Johnston Atoll chemical agent disposal system (JACADS) - Final Environmental Impact Statement, 1 Nov. 1983. Pacific Ocean Division, Corps of Engineers, Ft. Shafter, Hawaii, 75 p. + Appendices A-M.

U.S. Fish and Wildlife Service. MS. Pacific Islands National Wildlife Refuges: Johnston Atoll NWR, Baker Island NWR, Howland Island NWR, Jarvis Island NWR. U.S. Fish and Wildlife Service, Honolulu, Hawaii.

Votaw, H. C. 1943. Johnston Island. U.S. Naval Institute Proceedings, 69, 487:1176-1180.

Wetmore, A. 1925. Bird life among lava rock and coral sand. Natl. Geogr. Mag. 59:76-108.

MS. a. Field notes, 1923. [Unpublished manuscr.] Smithson. Inst., Wash. D.C.

MS. b. A scientific survey of Johnston Island, 1923, 25 p. [Unpublished manuscr. prepared in 1963.] [Page 5 missing from copy seen on file at the U.S. Fish and Wildlife Service, Honolulu.]

Whittle, K. J., R. Hardy, A. V. Holden, R. Johnson, and R. J. Pentreath. 1977. Occurrence and fate of organic and inorganic contaminants in marine animals. In H. F. Kraybill, C. J. Dawe, J. C. Harshbarger, and R. J. Tardiff (editors), Aquatic pollutants and biologic effects with emphasis on neoplasia, p. 47-79. New York Acad. Sci., N.Y.

Whittow, G. C., and G. H. Balazs. 1982. Basking behavior of the Hawaiian green turtle (Chelonia mydas). Pac. Sci. 36:129-139.

Witkowski, S. A., and J. G. Frazier. 1982. Heavy metals in sea turtles. Mar. Pollut. Bull. 13:254-255.

Woodbury, D. O. 1946. Builders for battle. E. P. Dutton and Co., N.Y., 415 p.

Table 1.--Results of turtle netting effort in meter-hours (MH).

Net location	Phase 1			Phase 2			Total		
	MH	MH per turtle	Number captured	MH	MH per turtle	Number captured	MH	MH per turtle	Number captured
1	4,460	1,115	4	1,975	1,975	1	6,435	1,287	5
2	509		0	4,206	526	8	4,715	589	8
3	1,085	362	3	3,513		0	4,598	1,533	3
4	567		0	--		--	567		0
5	1,026		0	--		--	1,026		0
6	216		0	--		--	216		0
7	--		--	2,748	550	5	2,748	550	5
8	--		--	280		0	280		0
9	--		--	400		0	400		0
10	--		--	340		0	340		0
11	--		--	949		0	949		0
12	--		--	820		0	820		0
13	--		--	153		0	153		0
14	--		--	340		0	340		0
15	--		--	420		0	420		0
16	--		--	420		0	420		0
17	--		--	189		0	189		0
Total	7,863	1,123	7	16,753	1,197	14	24,616	1,172	21

Table 2.--Daily turtle netting effort.

Date 1983	Net location	Number captured	Duration in hours	Length of net (m)	Netting effort (meter-hours)
Phase 1					
10/3-10/7	1	4	94.5	40	3,780
10/4-10/5	2		20	9	180
10/5-10/7	3	2	47	9	423
10/5-10/6	4		21	27	567
10/6-10/7	5		21	27	567
10/7-10/8	1		17	40	680
10/7-10/8	5		17	27	459
10/8-10/11	3	1	73.5	9	662
10/9-10/10	2		23.5	14	329
10/11	6		8	27	216
Subtotal		7			7,863
Phase 2					
11/4	3		10.5	40	420
11/4	2		10	27	270
11/5	2		10.5	40	420
11/5	1		8.5	40	340
11/5	3		6	27	162
11/6	2	2	9.5	27	257
11/6	3		9.5	40	380
11/6	7		7	40	280
11/6	8		7	40	280
11/7	7	1	10	40	400
11/7	9		10	40	400
11/7	2	1	8.5	27	230
11/7	3		8.5	40	340
11/8	2	1	9.5	27	257
11/8	3		9.5	40	380
11/8	7	2	8.5	40	340
11/8	10		8.5	40	340
11/9	3		10.5	40	420
11/9	11		10.5	40	420

Table 2.--Continued.

Date 1983	Net location	Number captured	Duration in hours	Length of net (m)	Netting effort (meter-hours)
11/9	2		9	27	243
11/9	1		9	40	360
11/10	1		9.5	40	380
11/10	2	2	9.5	40	380
11/10	3		8.5	46	391
11/10	11		8.5	40	340
11/11	2		10	40	400
11/11	7	2	10	40	400
11/11	12		10	40	400
11/11	3		10	18	180
11/11	1	1	5	27	135
11/12	2	1	10.5	18	189
11/12	3		10.5	40	420
11/12	7		10.5	40	420
11/12	12		10.5	40	420
11/12	2		8.5	77	230
11/13	1		8.5	40	340
11/13	2	1	8.5	27	230
11/13	7		8.5	40	340
11/13	13		8.5	18	153
11/13	14		8.5	40	340
11/14	1		10.5	40	420
11/14	2		10.5	40	420
11/14	11		10.5	18	189
11/14	7		10.5	27	284
11/14	15		10.5	40	420
11/15	2		10.5	40	420
11/15	3		10.5	40	420
11/15	7		10.5	27	284
11/15	16		10.5	40	420
11/15	17		10.5	18	189
11/16	2		6.5	40	260
Subtotal		14			16,753
Total		21			24,616

Table 3.--Tag numbers, capture sites, and straight carapace lengths of green turtles.

Tag No.[1]	Date 1983	Time of capture	Net location	Straight carapace length (cm): Midline to posterior of postcentral	Straight carapace length (cm): Midline to of notch
7451-55	10/4	0700	1	100.1	99.8
7485-89	11/6	1500	2	95.9	94.9
7565-69	11/13	1730	2	92.5	92.9
7461-65	10/5	1330	1	90.9	89.6
7490-94	11/7	1600	7	89.7	89.5
7500-04	11/8	1600	2	89.5	88.7
7512-16	11/10	0930	2	89.0	88.8
7468-72	10/6	1730	1	88.2	—
7456-60	10/4	1300	1	87.4	86.9
7560-64	11/12	1600	2	87.0	—
7473-75	10/7	1230	3	84.0	83.6
7521-25	11/11	1500	7	83.7	83.6
7517-20	11/10	1600	2	83.3	83.3
7495-99	11/7	1230	2	82.9	82.1
7555-59	11/11	1700	1	79.1	78.3
7476-80	10/11	1500	3	77.2	76.5
7509-11	11/8	1700	7	75.6	75.2
7505-08	11/8	1700	7	75.2	74.5
7551-54	11/11	1500	7	75.2	74.8
7481-84	11/6	1130	2	72.8	72.1
7466-67	10/5	1830	3	57.4	—

[1] Tag series used at Johnston Atoll--7451-7525 and 7551-7569.

Tag inscription reads: WRITE HIMB
UNIVERSITY
HAWAII, 96744

Table 4.--Body measurements and weights of green turtles.

Tag No.	Carapace length Straight (cm)	Carapace length Curved (cm)	Carapace width Straight (cm)	Carapace width Curved (cm)	Plastron length (cm)	Tail length (cm)	Head width (cm)	Weight (kg)
7451	100.1	107.8	83.2	105.5	81.1	25.6	13.5	--
7485	95.9	103.7	72.5	94.8	80.2	26.5	12.8	151.4
7565	92.5	96.7	72.1	96.0	79.3	26.4	12.6	141.8
7461	90.9	97.5	69.8	90.6	73.1	20.2	12.1	--
7590	89.7	94.5	71.6	88.5	67.5	[1]41.7	11.6	115.9
7500	89.5	96.0	68.8	85.5	72.4	25.2	11.9	--
7512	89.0	95.0	67.3	86.5	70.8	[1]54.6	12.3	114.1
7468	88.2	92.6	71.6	86.0	70.9	[1]44.0	12.1	--
7456	87.4	95.4	70.4	94.6	72.8	21.0	11.2	--
7560	87.0	92.6	67.4	85.3	70.6	21.2	12.0	108.6
7473	84.0	90.5	65.4	94.5	70.0	21.0	12.0	96.4
7521	83.7	92.2	62.2	80.0	67.2	[2] --	11.4	85.9
7517	83.3	87.2	64.6	82.0	68.2	[3] --	--	84.5
7495	82.9	89.2	65.4	80.6	68.3	18.2	11.3	87.7
7555	79.1	84.5	61.6	79.0	64.0	18.2	10.7	74.1
7476	77.2	84.5	59.6	82.0	61.2	14.5	10.2	67.7
7509	75.6	82.0	57.0	77.8	--	--	10.3	68.2
7505	75.2	81.5	57.8	75.5	60.4	17.0	9.9	65.0
7551	75.2	80.0	61.2	77.6	59.8	14.5	10.9	62.3
7481	72.8	79.1	58.1	76.2	59.3	12.5	9.7	63.6
7466	57.4	63.0	46.3	58.0	44.0	9.5	7.1	--

[1] Adult male.

[2] Short deformed tail--no indication of being a male.

[3] Adult male--tail partly amputated.

Table 5.--Front flipper measurements and scale counts of green turtles.

Tag No.	Straight carapace length (cm)	Flipper width[1] Left	Flipper width[1] Right	Flipper scales Left	Flipper scales Right	Postocular scales Left	Postocular scales Right
7451	100.1	14.1	14.4	7	6	3	4
7485	95.9	14.9	15.3	6	6	4	4
7565	92.5	14.0	14.3	6	6	4	4
7461	90.9	13.2	13.4	6	6	4	4
7490	89.7	13.6	13.5	6	6	4	4
7500	89.5	14.7	14.6	6	6	4	4
7512	89.0	15.4	15.0	6	6	4	4
7468	88.2	14.2	14.5	6	6	5	4
7456	87.4	12.4	12.6	5	5	4	4
7560	87.0	13.2	13.2	6	6	4	4
7473	84.0	13.4	13.2	6	6	4	4
7521	83.7	12.6	12.8	6	6	4	4
7517	83.3	14.7	14.6	6	6	4	4
7495	82.9	12.0	12.0	6	6	4	4
7555	79.1	13.1	13.1	6	6	5	4
7476	77.2	11.9	11.0	6	6	4	4
7509	75.6	12.4	12.0	6	6	4	5
7505	75.2	11.0	11.2	6	6	4	4
7551	75.2	12.0	11.2	6	6	4	4
7481	72.8	11.2	10.3	6	6	4	4
7466	57.4	--	--	6	6	4	4

[1] Straight line measurement taken from the anterior distal edge of the claw scale to the scale located directly across on the flipper's trailing edge (usually scale No. 6 counting proximal to distal along the trailing edge).

Table 6.--Sex determination of green turtles.

Tag No.	Straight carapace length (cm)	Tail length[1] (cm)	Testosterone level[2]	Sex
7451	100.1	25.6	--	Female
7485	95.9	26.5	≤11.1	Female
7565	92.5	26.4	--	Female
7461	90.9	20.2	--	Female
7490	89.7	41.7	11,248.6	Male
7500	89.5	25.2	<11.1	Female
7512	89.0	54.6	561.6	Male
7468	88.2	44.0	--	Male
7456	87.4	21.0	--	Female
7560	87.0	21.1	13.3	Female
7473	84.0	21.0	--	Female
7521	83.7	[3] --	13.9	Female
7517	83.3	[4] --	2,324.9	Male
7495	82.9	18.2	13.7	Female
7555	79.1	18.2	418.7	Male
7476	77.2	14.5	--	--
7509	75.6	--	--	--
7505	75.2	17.0	≤11.1	Female
7551	75.2	14.5	--	--
7481	72.8	12.5	26.1	Female
7466	57.4	9.5	≤11.1	Female
Total				13 Females 5 males

[1] Straight line measurement from the posterior midline edge of the plastron to the tip of the extended tail.

[2] Testosterone level in the blood in picograms per milliliter (10^{-12}g/ml).

[3] Short deformed tail--no indication of being a male.

[4] Adult male--tail partly amputated.

Table 7.--Identification of stomach contents sampled from green turtles.

Tag No.	Straight carapace length (cm)	Sex	Capture site (net location)	Contents
7451	100.1	Female	1	*Oscillatoria* sp. (trace filaments)
7565	92.5	Female	2	*Bryopsis pennata* var. *secunda* *Oscillatoria* sp. Unidentified amphipod.[1] *Pyxidula* sp. (diatoms-trace)
7461	90.9	Female	1	*Zonaria* sp. (trace-filament)
7512	89.0	Male	2	*Caulerpa racemosa* var. *uvifera* *Climocosphenia* sp. (diatoms-trace) *Oscillatoria* sp. (trace-filament)
7473	84.0	Female	3	Unidentified fibers-trace
7495	82.9	Female	2	*Climacosphenia* sp. (diatom-trace) Unidentified filamentous bacteria
7476	77.2	--	3	*B. pennata* var. *secunda*
7466	57.4	Female	3	*B. pennata* var. *secunda* *Polysiphonia* sp. (fragment)

[1] Probably originated from the esophagus.

Table 8.--Identification of mouth and fecal contents sampled from green turtles.

Tag No.	Straight carapace length (cm)	Sex	Capture site (net location)	Contents
Mouth contents				
7485	95.9	Female	2	*Caulerpa racemosa* var. *macrophysa* *Acrochaetium* sp. (epiphytic on *Caulerpa*)
7565	92.5	Female	2	*Bryopsis pennata* *Oscillatoria* sp. filaments *Pyxidicula* sp. (diatoms) Unidentified amphipod
7560	87.0	Female	2	*Bryopsis pennata* var. *secunda* *Pyxidicula* sp. (diatoms)
7555	79.1	Male	1	*Caulerpa racemosa* var. *macrophysa* Unidentified filamentous bacteria Unidentified blue-green algae
7481	72.8	Female	2	*Bryopsis pennata*
Fecal contents				
7509	75.6	--[1]	7	*Caulerpa racemosa* var. *uvifera* (75%) *Bryopsis pennata* (25%)

[1] Not determined.

Table 9.--Algae collected during diving surveys with scuba.

Dive No.	Date 1983	Location	Algae collected
10	10/10	J	*Bryopsis pennata* var. *secunda* (Harvey) Collins and Harvey *Caulerpa racemosa* var. *macrophysa* (Kutzing) Taylor *C. racemosa* var. *uvifera* (Turner) Weber von Bosse *C. serrulata* (Förskal) J. Ag.
11	10/11	K	*C. serrulata* f. *angusta* (Weber von Bosse) Taylor *C. serrulata* (Förskal) J. Ag. *Dictyota friabilis* Setchell (epiphytic on *Caulerpa*)
13	11/4	M	*Gelidium pusillum* *Ceraminium* sp. (trace)
14	11/5	N	*Caulerpa serrulata* *Avrainvillea lacerata* *Hydrocoleum lyngbyaceum* *Zonaria* sp. *Polysiphonia* sp. (trace)

Table 10.--Percent nutrient composition of principal food sources used by green turtles.[1]

Algae	Dry matter	Crude protein[3]	Ether extract	Ash	Neutral detergent fiber[2]	Acid detergent fiber[2]	
						Permanganic lignin	Cellulose
Bryopsis pennata var. *secunda* (from foraging site)	7.0	23.8	2.0	38.2	25.6	2.7	7.9
B. pennata var. *secunda* (detached)	7.1	25.7	2.6	33.8	27.8	3.3	11.3
Caulerpa racemosa var. *uvifera*	3.9	8.0	0.7	61.4	24.6	6.3	6.3
C. racemosa var. *macrophysa*	3.7	9.1	0.9	63.8	25.5	6.5	7.5

[1] Reported on a dry matter basis as determined by the "proximate analysis" method commonly used for terrestrial animal forage.

[2] Present in benthic algae as a complex polysacchride; not true lignin or cellulose as found in terrestrial plants.

[3] Nitrogen x 6.25.

Table 11.--Mineral composition of principal food sources used by green turtles.[1]

Algae	Ca	P	K	Mg	Na	Fe	Cu	Mn	Zn
	%					ppm			
Bryopsis pennata var. *secunda* (foraging site)	2.00	0.27	0.94	1.06	11.10	110	8	19	57
B. pennata var. *secunda* (detached)	1.82	0.23	0.93	0.95	10.00	88	10	17	66
Caulerpa racemosa var. *uvifera*	2.45	0.10	1.07	0.41	19.36	90	9	9	76
C. racemosa var. *macrophysa*	0.87	0.10	1.28	0.31	22.00	2,558	11	29	81

[1] Dry matter basis. Ca = Calcium; P = Phosphorus; K = Potassium; Mg = Magnesium; Na = Sodium; Fe = Iron; Cu = Copper; Mn = Manganese; Zn = Zinc.

Table 12.--Identification of epizoites sampled from green turtles.

Tag No.	Sex	Straight carapace length (cm)	Epizoites
7485	Female	95.9	*Acrochaetium* sp. *Polysiphonia tsudana* *Lyngbya semiplena* Unidentified roundworms Unidentified amphipods Unidentified black "mites"
7565	Female	92.5	*Acrochaetium* sp. *Polysiphonia tsudana* *L. semiplena* *Sphacelaria tribuloides* *Urosopora* sp. *Pilinia* sp.[1] Unidentified foraminifera
7512	Male	89.0	*Acrochaetium* sp. *Polysiphonia tsudana* *L. semiplena* *Urospora* sp. *Pilinia* sp.[1] *Chadophora* sp. (trace) *Dermocarpa sphaerica* (epiphitic on *Chadophora* sp.)
7495	Female	82.9	Same as tag No. 7485
7481	Female	72.8	*Polysiphonia tsudana* *L. semiplena* *Urospora* sp. *Pilinia* sp.[1]

[1] Possibly *Pilinia rimosa* Kutzing, which may be a new record for the tropical Pacific.

Table 13.--Red blood cell cholinesterase values for nine green turtles.

Tag No.	Straight carapace length (cm)	Weight (kg)	Net location	Sex[1]	Cholinesterase[2]
7485	95.9	151.4	2	Female	0.15 0.16
7490	89.7	115.9	7	Male	0.27 0.27
7500	89.5	—	2	Female	0.13
7512	89.0	114.1	2	Male	0.23
7517	83.3	84.5	2	Male	0.29 0.30
7495	82.9	87.7	2	Female	0.14 0.13
7555	79.1	74.1	1	Male	0.32 0.34
7505	75.2	65.0	7	Female	0.26
7481	72.8	63.6	2	Female	0.28 0.31

[1] Based on testosterone level.

[2] Decrease in pH units (pH/h) using a 0.2 ml aliquot.

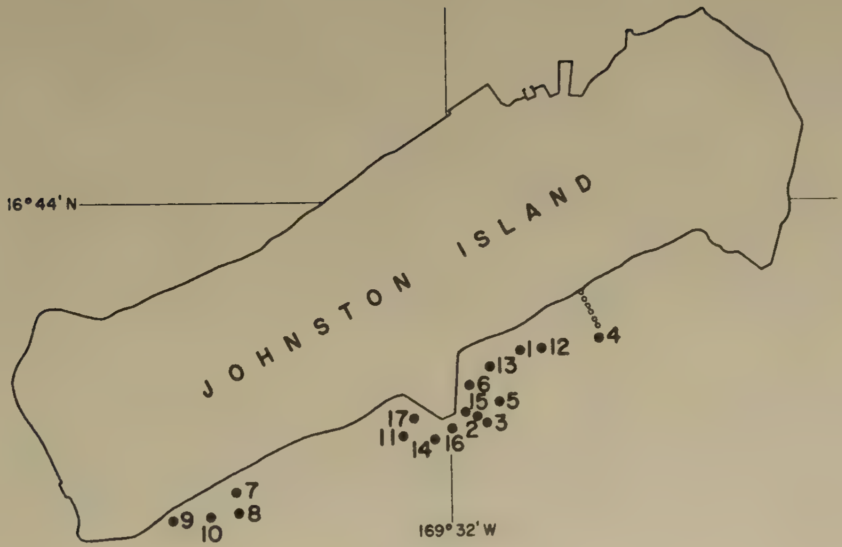
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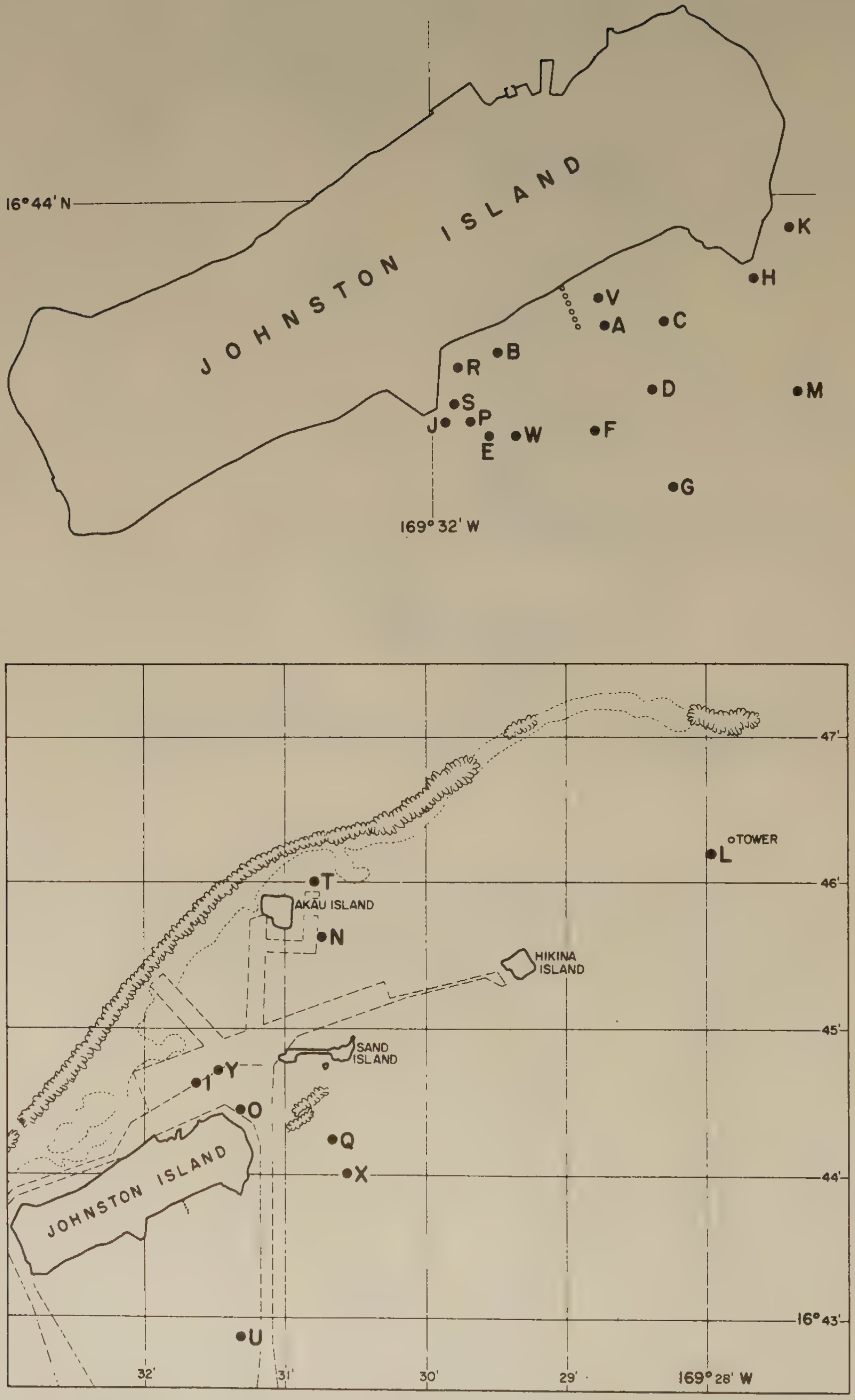
Figure 1.--Location of turtle nets.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169° 28' W

Figure 2.--Central location of 26 diving surveys with scuba. The bottom areas actually covered extend out in concentric circles from each location and overlap considerably for many dives.

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Marine Turtle Newsletter

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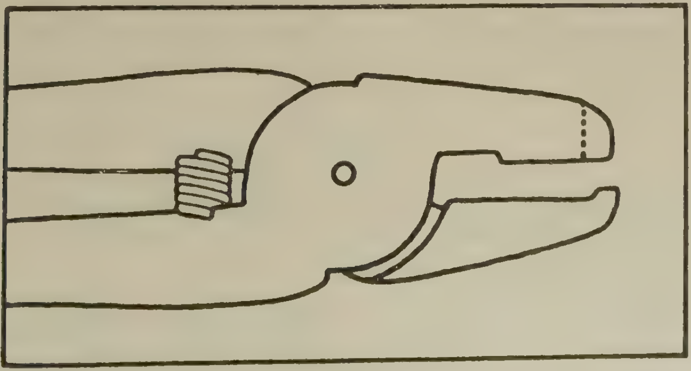
A SUGGESTED MODIFICATION OF TAGGING PLIERS

The unnecessary bruising of tissue when tagging sea turtles is undesirable because increased tag loss could occur and the behavior of the turtles might be adversely altered, especially while they are nesting, by an overly painful tagging experience. For example, if the behavior of a nesting turtle is modified by painful tagging, less soil might be deposited over the egg clutch, thereby changing incubation temperature and hatchling sex ratios. Other problems of tagging and tag retention have been discussed earlier (MTN 20:11-14).

Application of the National Band and Tag Company size 681 tag frequently results in severe pinching of tissue and pain (as evidenced by a sudden response) because of the small gap at the jaw tips of the tagging pliers when they are in the closed position. This tissue compression problem occurs when the thickness of the flipper exceeds the 4 mm gap between the jaw tips. For the Hawaiian green turtle, this commonly involves individuals approximately 50 cm or more in straight carapace length, depending on the exact tagging site.

Tagging pliers for the size 681 tag can be easily modified to eliminate or reduce this problem by grinding off the upper tip of the jaw, as shown in the accompanying diagram. The alteration does not seem to affect adversely the performance of the pliers in locking the tag properly. Over 200 turtles have now been tagged in Hawaii with modified tags. A similar modification may be possible on tagging pliers used with other tag types and sizes to avoid unnecessary crushing of tissue. Of course, caution should be exercised as with any change of equipment or procedure until it can be determined that the modification fulfills the individual's specific research needs.



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8512

VARIABILITY, TRENDS, AND BIASES IN REPRODUCTIVE RATES OF SPOTTED DOLPHINS, *STENELLA ATTENUATA*

Jay Barlow[1]

ABSTRACT

Temporal changes were examined in three parameters that affect reproduction of spotted dolphin populations in the eastern Pacific. Of mature females, percent pregnant decreased markedly from the period 1971-73 to the period 1974-83. Within the period 1974-83, percent pregnant remained relatively constant. Of pregnant females, percent lactating increased during the period 1971-83. The percentage of sexually mature females did not change. Potential biases in the measurement of the three parameters were identified by examining the effects of sampling conditions. The percentage of mature females that are pregnant and the percentage of pregnant females that are lactating were found to be robust to sampling conditions. The percentage of mature females in a sample was found to depend significantly on the number of dolphins killed per set, and annual variability was too large to be explained by random sampling error. Comparisons between two populations show that the more exploited population has a lower percent pregnant, although the opposite might be expected from density compensatory effects. Percent lactating and percent immature were higher in the more exploited population.

Changes in the reproductive parameters of cetacean populations can be used to make inferences about the status or general "health" of a population. For instance, increases in pregnancy rates and decreases in the age at attainment of sexual maturity were linked to reductions in Antarctic whale populations (Gambell 1975). Re-analysis of these data, however, revealed unsuspected biases, and Gambell's results are now being questioned (Mizroch 1983). The purpose of this paper is to examine potential biases in measuring reproductive rates of spotted dolphins, *Stenella attenuata*. This species is taken incidentally in the tuna purse seine fishery in the eastern tropical Pacific (Smith 1983). The intent is to determine whether reproductive rates can be measured with sufficient precision to monitor intrapopulation changes or to make interpopulation comparisons.

Previous studies of female reproduction in spotted dolphins of the eastern Pacific have shown an apparent decrease in pregnancy rates from 1973 to 1975 (Perrin et al. 1977), from 1973 to 1978,[2] and from 1971 to 1978 (Hester 1984). Hester (1984) suggested that this decline in pregnancy rates is related to the decline in fishing-related dolphin mortality during the same time period.

Three indices of the reproductive status of female spotted dolphins are examined in the present paper: 1) the fraction of sexually mature individuals that are pregnant, 2) the fraction of pregnant females that are lactating, and 3) the fraction of females that are sexually mature. These measures have been used previously in calculating what has been termed the gross annual reproductive rate (GARR) of spotted dolphins (Perrin et al. 1976). This paper reexamines data from 1971 to 1978 plus additional data from 1979 to 1983 to determine whether the previously noted trends in reproductive rates are real, and if so, whether they are continuing. Also, factors are examined which may be biasing estimates of reproductive rates and which could be causing spurious changes in apparent pregnancy rates and GARR. Finally, differences in these reproductive indices between two geographic stocks of spotted dolphin are discussed in view of their different histories of incidental fishing mortality.

MATERIALS

Reproductive data were collected from a sample of the dolphins killed in tuna purse-seining operations in the eastern tropical Pacific (ETP). Three stocks of spotted dolphins are recognized in this area based on morphological differences (Perrin et al. 1979). Samples considered here include two of these: the northern offshore stock which has been subject to tuna fishing since 1959 and the southern offshore stock which has been subject to exploitation since

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2] Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rate of gross annual reproduction in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-78. Admin. Rep. LJ-80-02, 51 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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the early 1970's. In 1971 and 1972, field technicians collected samples predominantly from females with the "adult" or fused color pattern (Perrin 1970). Beginning in 1973, field technicians were instructed to collect samples nonselectively with respect to size and sex. Operationally, this meant working-up specimens in the order in which they appeared on the deck of the tuna vessel. Sampling methods and laboratory procedures are described in detail by Perrin et al. (1976). Sample locations are shown in Figure 1.

Reproductive tracts of mature and nearly mature females were preserved in the field for laboratory examination. In 1971 and 1972, the definition of "mature and nearly mature" was not explicit. In 1973, "mature and nearly mature" was defined as individuals with "mottled" or "fused" developmental color phases (Perrin 1970). Because females in the younger "speckled" color phase occasionally were found to be pregnant, "mature and nearly mature" was redefined operationally (beginning in 1974) as specimens >150 cm total length (TL, measured from tip of rostrum to fluke notch). Laboratory examination of preserved ovaries was used to determine the presence of corpora from past ovulations. Pregnancy was determined by visual examination of the uterus (in later years, fetuses >30 cm TL were removed and measured in the field). Mammary glands were slit and checked in the field for the presence of milk.

In addition to the above life history information, field technicians collected data pertaining to conditions under which the samples were taken. Information used in this report includes the observer's estimate of the size of the school from which the sample was taken, the duration of the chase before the net was set, the number of dolphins known to be killed during fishing operations, and the geographic location at which the sample was taken.

METHODS

Three indices of female reproduction are considered in this paper: the percent pregnant, the percent lactating, and the percent mature. Temporal trends in these three indices were examined by regressing annual means against year (weighting by the inverse of binomial variances).

In calculating the percentages of mature females that were pregnant and that were lactating, specimens were used only if both ovaries were collected and if at least one corpus of ovulation (corpus albicans or corpus luteum) was present. Previously, 1971 and 1972 samples were excluded from calculation of percent pregnant because of undersampling of younger females with a mottled color pattern (Perrin et al. 1977). This was not deemed necessary in this study, because in 1973-83 samples the percent pregnant for mature mottled females (31.1%) was essentially the same as that for mature females with a fused color pattern (31.4%).

In calculating the percentage of females that were sexually mature, two different criteria were used for determining maturity. In the majority of cases both ovaries were examined, and the presence of one (or more) corpus of ovulation was taken as evidence of sexual maturity. If ovaries were not collected or examined (which was true for about 30% of females over 150 cm TL), a length criterion was used for maturity. Samples from 1971 and 1972 were excluded from these analyses because sampling was not random in those years.

"Length at attainment of sexual maturity" was determined by the method used by Perrin et al. (1977). Based on the sample for which ovaries were examined, this length was estimated as the length at which the number of longer immature individuals equals the number of shorter mature individuals. For the northern stock, the length at the onset of sexual maturity was determined independently for each year 1974-83 (176.5, 177.5, 177.0, 177.0, 178.0, 177.5, 179.0, 178.5, 180.0, and 182.0 cm, respectively). In 1973 the decision to collect ovaries was not based on specimen length. The apparent trend in these data yields a significant regression ($P = 0.0008$); hence, regression estimates were substituted for annual estimates for 1974-83, with an extrapolation to 1973. These values were 175.6, 176.1, 176.6, 177.1, 177.6, 178.0, 178.5, 179.0, 179.5, 180.0, and 180.5 cm, respectively, for 1973-83. For the southern stock, insufficient data exist to calculate a length at attainment of sexual maturity for individual years, hence the collective value was used for all years (175.0 cm).

Six factors were examined to determine whether annual changes in the above percentages of pregnant females were caused or affected by changing biases in the sampling methods. These factors include 1) geographical provenance, based on two strata (Fig. 1) which roughly correspond to the historical tuna fishing grounds (inside the Commission Yellowfin Regulatory Area, CYRA) and a more recently exploited area (outside the CYRA); 2) the quarter of the year; 3) the length of chase, or the time between sighting the dolphin school and capture (net set); 4) the observer's estimate of the dolphin school size (only available since 1973); 5) the number of dolphins known to have been killed in the set; and 6) the total number of tons of tuna caught in the set.

The selection of these six factors was guided to

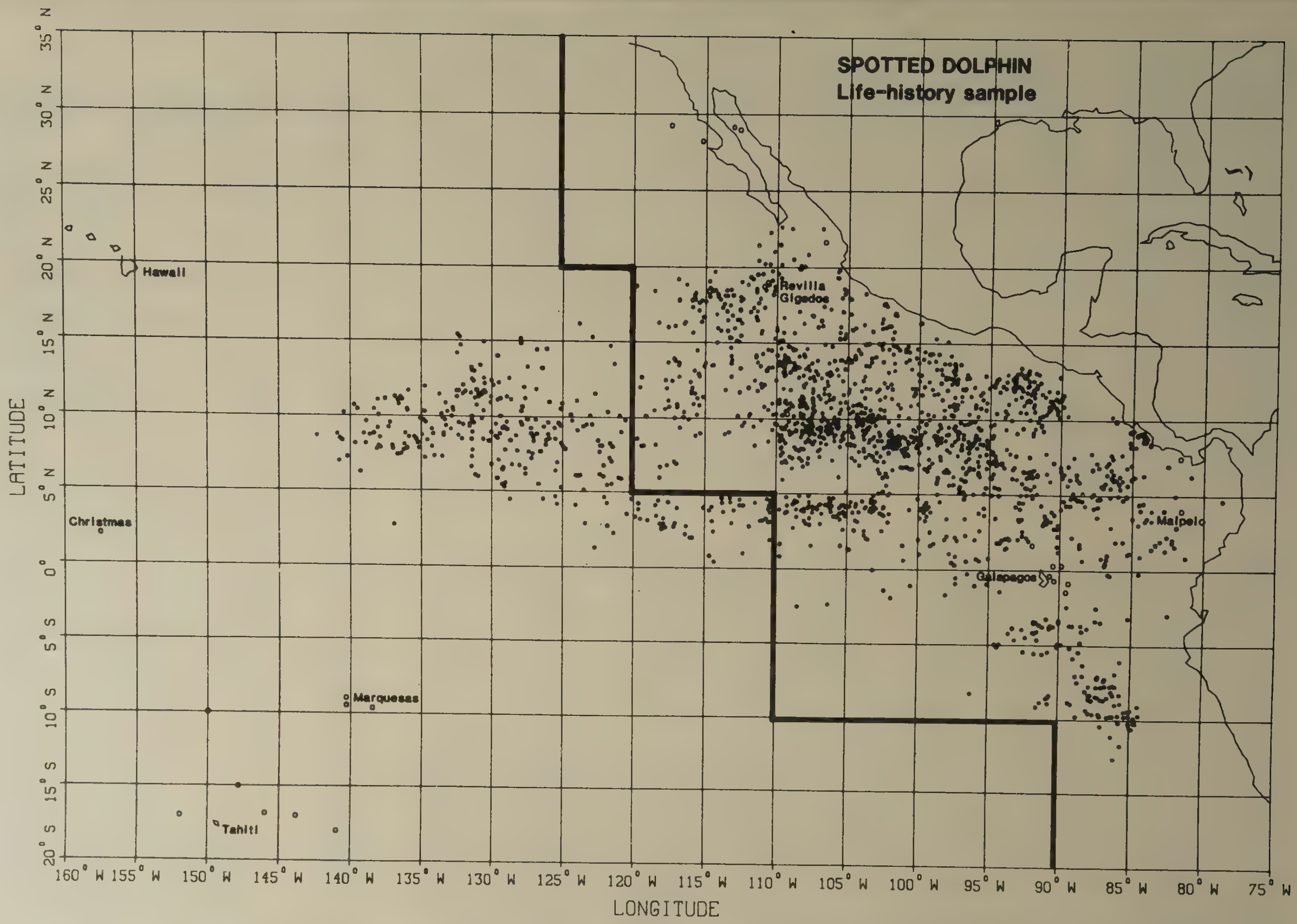
SPOTTED DOLPHIN
Life-history sample
Hawaii
Christmas
Marquesas
Tahiti
Revilla Gigedos
Galapagos
Malpelo
LATITUDE
35° N
30° N
25° N
20° N
15° N
10° N
5° N
0°
5° S
10° S
15° S
20° S
LONGITUDE
160° W
155° W
150° W
145° W
140° W
135° W
130° W
125° W
120° W
115° W
110° W
105° W
100° W
95° W
90° W
85° W
80° W
75° W

FIGURE 1.—Locations at which male and female spotted dolphins were collected for life history studies, 1968-83. Bold line indicates western border of the Commission Yellowfin Regulatory Area (CYRA). Figure taken from Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass. 1984. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Admin. Rep. LJ-84-02, available from NOAA, Southwest Fisheries Center, La Jolla, CA 92038.

some extent by previous studies. The sex ratio and the fraction of yearling dolphins in a sample were found to vary with kill size (No. 5 above). The fraction of neonatal animals in tuna-vessel samples was found to vary significantly with area, season, chase time, dolphin kill, and tuna catch (Nos. 1, 2, 3, 5, and 6 above)[3]. Preliminary work by A. A. Hohn[4] and M. D. Scott[5] has indicated that immature spotted dolphins may segregate into schools with different characteristic school sizes (No. 4 above).

The significance of each of the above factors was tested separately using a Pearson chi-square. For each test, the null hypothesis was that either percent pregnant, percent lactating, or percent mature is independent of the factor being tested. If this hypothesis is shown to be false, then it is likely that reproductive parameters may be affected by sampling bias. Unfortunately, the above sampling factors are not independent; a factor may appear significant when, in fact, that factor is merely correlated with a causative factor. Because of this, probablilties should be interpreted with caution.

Multiway comparisons were used to discriminate factors which are truly important from those which are correlated to significant factors. A hierarchical approach was used, based on the log-linear model for discrete multivariate analysis (program BMDP4F, Dixon 1981). The above 2-way tests were used to identify factors that may be significant. The factors that were significant in the 2-way tests were used in 3-way tests. The factors which proved significant in the 3-way tests were then included in 4-way tests (which proved to be a practical upper limit on multiway tests using our data set). In this manner, multiway comparisons of factors could be tested, whereas a 7-way test of all factors would not have been feasible.

Analysis of variance (ANOVA) was tried and rejected as an alternative to the log-linear model for multiway comparisons. The method used in this trial was to calculate percent pregnant for each set and to use sets as replicates in an ANOVA. Although ANOVA is recognized to be robust to violations in assumptions, the sample size for individual sets is very small (mean number of mature females per set is 1.6, mode is 1). As a result, the percent pregnant in 72% of sets was either 0% or 100% of mature females. No transformation was able to normalize these data. Using an arc-sine transformation, 2-way ANOVA was not even able to recognize the four significant factors affecting percent pregnant that were identified using a simple Pearson chi-square. Because of these problems, the ANOVA model was rejected for use in the multiway comparisons.

RESULTS

Percent Pregnant

The fractions of sexually mature females that were pregnant are given in Table 1 for the samples of the northern and southern offshore stocks collected from 1971 to 1983. Sample sizes decline in the later years for the northern stock, but are typically >100.

TABLE 1.—Fractions a) of females that were sexually mature, b) of sexually mature females that were pregnant, and c) of pregnant females that were lactating. Samples include 1971-83 specimens from the northern and southern offshore stocks of spotted dolphins. Fraction mature was not sampled in 1971 and 1972.

	Year													
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	Overall
Northern stock														
a) Fraction mature			0.56	0.53	0.54	0.50	0.61	0.59	0.59	0.55	0.61	0.56	0.50	0.561
Number in sample			1,149	1,013	1,215	751	995	564	593	509	465	579	137	7,970
b) Fraction pregnant	0.48	0.41	0.42	0.29	0.29	0.34	0.27	0.24	0.30	0.30	0.29	0.32	0.38	0.329
Number mature	79	449	573	487	493	291	375	229	205	148	153	148	37	3,667
c) Fraction lactating	0.26	0.08	0.08	0.17	0.14	0.13	0.35	0.15	0.30	0.23	0.24	0.19	0.28	0.162
Number pregnant	38	180	236	138	130	93	94	52	61	43	42	47	14	1,168
Southern stock														
a) Fraction mature			0.58	—	0.68	0.63	0.61	0.77	0.58	0.73	0.60	0.70	0.69	0.656
Number in sample			24	0	38	254	23	51	166	59	20	199	106	940
b) Fraction pregnant	—	—	0.75	—	0.49	0.48	0.12	0.28	0.22	0.35	0.00	0.32	0.18	0.364
Number mature	0	0	12	0	23	145	8	25	60	17	8	73	22	393
c) Fraction lactating	—	—	0.00	—	0.22	0.04	0.00	0.16	0.08	0.00	—	0.23	0.00	0.087
Number pregnant	0	0	9	0	9	68	1	6	13	6	0	22	4	138

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[3] Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, 7 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[4] A. A. Hohn, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

[5] M. D. Scott, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

Samples sizes for the southern stock are highly variable between years, and several years have too few specimens to reliably estimate the fraction of the population that would be pregnant. For 1973-83, the overall percentage of pregnant females is, however, significantly higher for the southern stock, 36.4%, than for the northern stock, 31.4% (χ_1^2 = 3.97, P = 0.05). Because of this difference, northern and southern stocks were not pooled in subsequent analyses. Due to the small sample size from the southern stock, examination of trends and biases in female reproductive rates was limited to the northern stock.

Annual estimates of the percentage of pregnant females are illustrated in Figure 2 for the northern offshore stock. The regression is significant; however, the residuals do not appear randomly distributed. The negative slopes of the regression lines are largely due to high pregnancy rates in 1971-73. Expected values for the percent pregnant in each year were generated in two ways: from the overall percent pregnant and from the "de-trended" regression predictions. Chi-square tests using these expected values show the annual variability in percent pregnant is greater than would be expected from random sampling of a population with a constant ($P < 0.001$) or linearly decreasing ($P < 0.001$) pregnancy rate.

Although natural year-to-year variability in pregnancy rates cannot be ruled out, a changing bias in sampling could also cause larger than expected variability in percent pregnant. To look for such a bias, the sample from the northern stock was stratified by the six sampling factors described above. The percent pregnant in each of these strata is given in Table 2, with the chi-square probabilities that the samples could have been drawn randomly from the pooled sample. Of the factors examined, pregnancy rate was significantly related to sampling season, dolphin kill-per-set, and tuna catch-per-set (henceforth the latter two are referred to as kill and catch).

Because sampling seasons, mean dolphin kills, and mean tuna catches vary significantly between years, these factors cannot be considered independent of year. For instance, the interaction between pregnancy rates and dolphin kill might appear significant due to high kill rates or high catch rates in a year (or years) that coincidentally had high pregnancy rates. Conversely, high pregnancy rates in one year may be due to a sampling bias related to dolphin kill.

Multiway tests were used to identify possible interactions between the three significant factors and year effects. In all cases, 3-way tests indicate that year effects are significant (Table 3). First order effects of kill, catch, and season were not significant; however, higher order effects involving the latter two were important (Table 3). A 4-way test using catch, season, and year also shows significant higher order interactions involving both catch and season (Table 3).

Higher order interactions involving year and another factor indicate that effect of that factor changes with year. Since pregnancy rates appear to have changed markedly from 1971-73 to 1974-83 (Fig. 2), the effect of the significant factors was

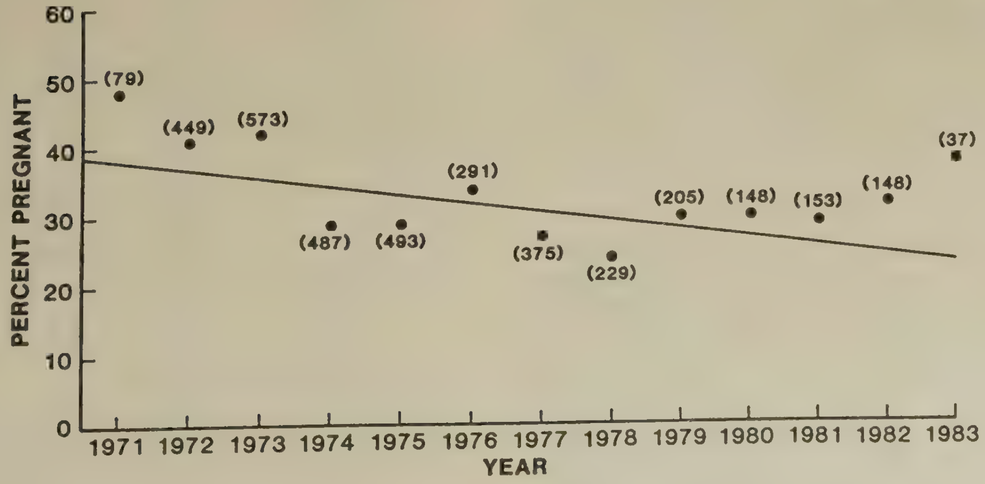

FIGURE 2.—Percentages of mature females that were pregnant for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid line represents weighted regression. Sample sizes are in parentheses.

TABLE 2.—Percentage of sexually mature females that were pregnant (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Pregnant (%)	*N*	Probability
1) Geographic area			
Inside CYRA	33.5	3,032	0.09
Outside CYRA	30.0	633	
2) Season			
1st quarter	34.7	1,799	0.04
2d quarter	33.5	741	
3d quarter	28.9	584	
4th quarter	30.4	542	
3) Chase time (min)			
<20	31.2	1,081	0.09
20-40	34.8	1,440	
>40	31.1	747	
4) School size			
<500	30.2	443	0.49
500-1,500	29.8	741	
>1,500	27.4	693	
5) Number killed			
1-10	29.8	1,104	<0.001
11-30	30.1	917	
>30	37.4	1,301	
6) Tuna caught (tons)			
0-5	29.0	428	0.02
6-15	33.0	848	
16-30	30.4	760	
>30	35.6	1,280	

tested separately for these two time periods. When the years 1971-73 were excluded (Table 4), the interactions between percent pregnant and season, dolphin kill, and tuna catch are no longer significant. When tests are performed on data from 1971 to 1973 alone (Table 4), season and tuna catch are still significantly related to pregnancy rate.

Percent Lactating

Annual trends in percent lactating for the northern stock of spotted dolphins are illustrated in Figure 3. Two cases are considered: 1) the percentage of all mature females that are lactating and 2) the percentage of pregnant females that are lactating. For both cases, a weighted regression shows a significant increase in the fraction of lactating females through time ($P < 0.05$). In the former case, the regression again appears to be driven by anomalous values in 1971-73. Percentages and sample sizes for the latter case are presented in Table

TABLE 3.—Multiway tests of factors affecting percent pregnant. Log-likelihood chi-square was used to calculate the probability that percent pregnant is independent of the stated factor(s) using the log-linear model. Pregnancy state (pregnant/not pregnant) is implicit as the first factor in each comparison.

Tests	Probability
3-way	
a) Year	<0.0001
Season	0.70
Year × season	<0.0001
b) Year	<0.0001
Kill	0.09
Year × kill	0.31
c) Year	<0.0001
Catch	0.14
Year × catch	0.0004
4-way	
Year	<0.0001
Season	0.90
Catch	0.15
Year × season	<0.0001
Year × catch	0.0002
Season × catch	0.003
Year × season × catch	0.07

TABLE 4.—Percentage of sexually mature females that were pregnant, grouped by season, dolphin kill, and tuna catch. The years 1971-73 and 1974-83 are grouped separately. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included.

Year	Pregnant (%)	*N*	Probability
1971-73 overall	41.9	1,101	
Season			
1st quarter	44.0	722	<0.001
2d quarter	47.6	210	
3d quarter	—	0	
4th quarter	25.4	169	
Number killed			
1-10	38.0	171	0.23
11-30	39.5	248	
>30	44.1	651	
Tuna caught (tons)			
0-5	37.6	101	0.04
6-15	44.5	247	
16-30	35.0	226	
>30	45.5	490	
1974-82 overall	29.0	2,566	
Season			
1st quarter	28.4	1,077	0.39
2d quarter	27.9	531	
3d quarter	28.9	584	
4th quarter	32.7	373	
Number killed			
1-10	28.3	933	0.27
11-30	26.6	669	
>30	30.6	650	
Tuna caught (tons)			
0-5	26.3	327	0.76
6-15	28.3	601	
16-30	28.5	534	
>30	29.5	790	

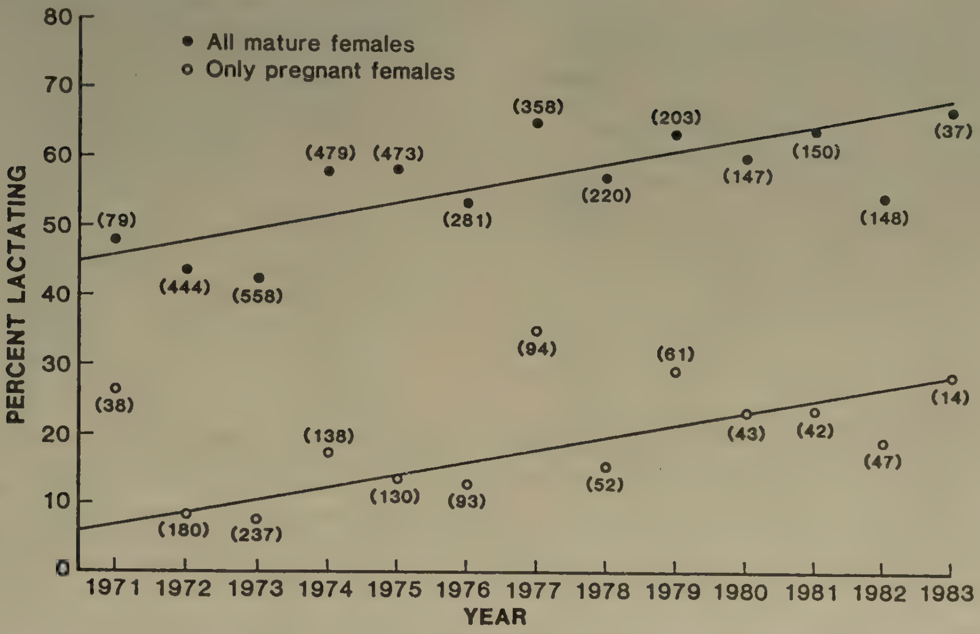

FIGURE 3.—Percentages of mature females that were lactating and percentages of pregnant females that were lactating for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid lines represents weighted regressions. Sample sizes are in parentheses.

1 for both the northern and southern stocks. Again sample size for the southern stock is too small to examine individual years; however, the overall percent of pregnant females that were lactating in 1973-83 samples shows significant differences between stocks ($\chi_1^2 = 6.50$, $P = 0.01$). Annual variability for the northern stock is greater than expected from random sampling of a population with a constant percent lactating ($\chi_{12}^2 = 63.5$, $P < 0.001$).

When the sample of pregnant females from the northern stock is stratified by the six sampling factors, lactation state was significantly related to sampling season, dolphin kill, and tuna catch (Table 5). Again, 3-way tests showed that the first order effect of these factors was not significant when year was included as the third factor (Table 6). In each of these cases, the first order effect of year was important. In one case, dolphin kill, a second order interaction between kill and year was also significant.

Percent Mature

The fractions of females that were sexually mature are given in Table 1 by stock and by year (1973-83). Again the sample sizes are sufficient in all years for the northern stock but are inadequate in some years for the southern stock. The southern stock is significantly different from the northern stock in percent mature ($\chi_1^2 = 31.2$, $P < 0.001$), and (given its small sample size) the southern stock was excluded in subsequent stratifications.

The percentage of all females that are mature from 1973 to 1983 is illustrated in Figure 4 for the northern stock. In this case, the weighted regression is not significant. Using chi-square tests, the level of annual variability in percent mature is larger than would be expected from randomly sampling a population with a constant fraction of mature females ($P < 0.001$).

For long-lived animals such as dolphins, annual variability in percent mature should be small and changes in this population parameter should be gradual. Since the annual variability observed in the data is larger than would be expected from random sampling error, year-to-year changes in sampling biases are likely. Percent mature was found to be significantly related to three of the six sampling factors examined: sampling season, dolphin kill-per-set, and tuna catch-per-set (Table 7).

Each of these three significant factors was tested with maturity state and year using 3-way tests (Table 8). For each of these factors, year was a significant factor and all other first order effects were not significant. Only dolphin kill showed a significant second order interaction with year.

TABLE 5.—Percentage of pregnant dolphins that were lactating (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Lactating (%)	N	Probability
1) Geographic area			
Inside CYRA	15.7	988	0.30
Outside CYRA	18.8	181	
2) Season			
1st quarter	11.9	611	
2d quarter	17.2	239	<0.001
3d quarter	26.7	161	
4th quarter	20.3	158	
3) Chase time (min)			
<20	14.8	331	
20-40	14.0	479	0.27
>40	18.6	226	
4) School size			
<500	20.0	130	
500-1,000	18.0	211	0.87
>1,500	19.7	183	
5) Number killed			
1-10	19.1	319	
11-30	16.5	267	0.03
>30	12.3	471	
6) Tuna caught (tons)			
0-5	20.5	117	
6-15	16.4	275	0.17
16-30	16.7	221	
>30	12.8	444	

DISCUSSION

Changes in the reproductive status of the female segment of a population can be monitored using a variety of reproductive indices: 1) mean age at sexual maturation, 2) mean length (or weight) at sexual maturation, 3) annual pregnancy rates, 4) calving interval, 5) percentage of mature females that are pregnant, 6) percentage of females that are lactating, and 7) percentage of females that are sexually mature. Changes in each of these are examined below.

Changes in Maturation Parameters

TABLE 6.—Multiway tests of factors affecting the percentage of pregnant females that are lactating. Log-likelihood chi-square was used to calculate the probability that percent lactating is independent of the stated factor(s) using the log-linear model. Lactation state (lactating/not lactating) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	<0.0001
Season	0.29
Year × season	0.007
b) Year	<0.0001
Kill	0.79
Year × kill	0.51

TABLE 7.—Percentage of female dolphins that were sexually mature (1973-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Mature (%)	N	Probability
1) Geographic area			
Inside CYRA	55.7	6,329	0.19
Outside CYRA	57.5	1,625	
2) Season			
1st quarter	54.2	3,495	
2d quarter	57.2	1,738	0.02
3d quarter	58.2	1,580	
4th quarter	57.6	1,155	
3) Chase time (min)			
<20	54.4	2,067	
20-40	56.1	3,084	0.36
>40	56.5	1,689	
4) School size			
<500	53.5	1,183	
500-1,500	56.8	1,970	0.19
>1,500	56.0	1,753	
5) Number killed			
1-10	57.9	2,465	
11-30	54.9	2,068	0.02
>30	54.0	2,321	
6) Tuna caught (tons)			
0-5	53.3	920	
6-15	55.1	1,779	0.05
16-30	54.5	1,668	
>30	57.7	2,482	

Myrick et al. (1984) have found no significant difference in the age at sexual maturation (ASM) between a sample from 1973 to 1978 and another sample from 1981. In the present study, length at attainment of sexual maturity is estimated to have increased 4.4 cm from 1974 to 1983. If these results hold, dolphins must be growing faster in recent years. Given small sample sizes of aged individuals, significant changes in ASM may be difficult to detect. Previous studies have shown that the age at sexual maturation is quite responsive to population changes in marine mammals (Fowler 1984), while length at maturation tends to show little change. For fin whales, *Balaenoptera physalus*, Lockyer (1972)

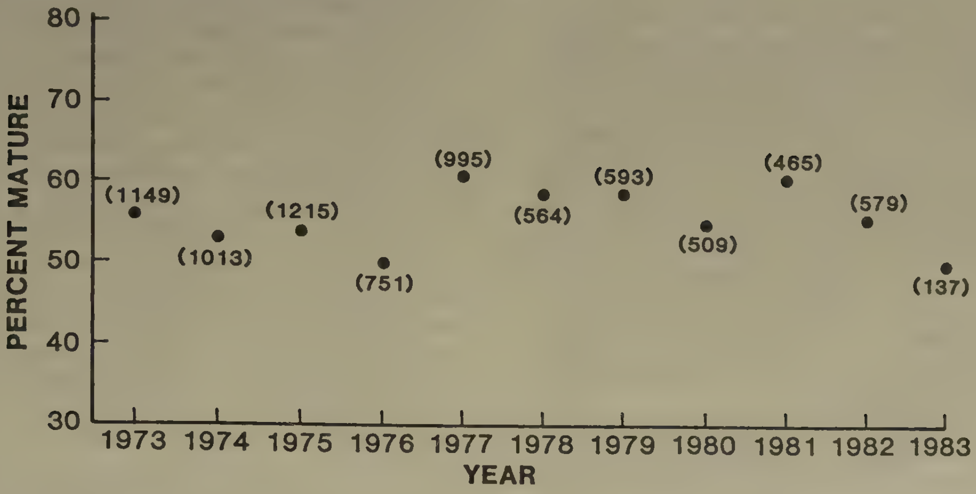

FIGURE 4.—Percentages of all females that were mature for the northern offshore stock of spotted dolphins from 1971 to 1983. Sample sizes are in parentheses.

TABLE 8.—Multiway tests of factors affecting percent mature. Log-likelihood chi-square was used to calculate the probability that percent mature is independent of the stated factor(s) using the log-linear model. Maturation state (mature/not mature) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	0.003
Season	0.49
Year × season	0.08
b) Year	0.003
Kill	0.16
Year × kill	0.002
c) Year	0.0009
Catch	0.09
Year × catch	0.42

showed a decrease in ASM without any change in the length at which maturity is attained. Laws (1956) predicted an inverse relationship between ASM and early growth rates for marine mammals. Spotted dolphins appear to show an increase in length at maturation with no change in ASM, and thus do not follow predicted patterns.

Trends in Percent Pregnant

Annual pregnancy rates, calving interval, and percent pregnant all measure essentially the same thing. Annual pregnancy rate and calving interval require knowledge of gestation times. Because density compensatory responses have not been shown in cetacean gestation times, it is more straightforward to deal directly with percent pregnant.

What appeared to be a rapid decline in dolphin pregnancy rates from 1973 to 1978 (Henderson et al. fn. 2), now appears as two eras with distinctly different pregnancy rates. The fraction of pregnant females in the 1971-73 samples was quite high. The 10 years since 1973 show a lower and relatively constant fraction of pregnant females. This difference in results is due largely to use of a larger sample size and a longer time series.

There is no evidence of the sort of slow, long-term trends in pregnancy rates that might be associated with changes in population sizes. The reason for the dramatic change in pregnancy rates between 1973 and 1974 is not known. At least three hypotheses could be used to explain this change: 1) it was the result of a naturally high pregnancy rate in 1971-73; 2) it was the result of heavy fishing-related mortality of nursing calves prior to 1974 that resulted in artificially high pregnancy rates; or 3) it was the result of a bias in the sampling by tuna vessels.

The first hypothesis suggests that changing environmental conditions result in annual changes in pregnancy rates. In the ETP the largest environmental perturbations are associated with "El Niño" events which occur on the time scale of from 5 to 10 yr (Rasmusson and Carpenter 1982). El Niño conditions prevailed in 1972 (moderate), 1975-76 (weak), and 1982-83 (very strong). These dates do not help explain the change in pregnancy rates that occurred between 1973 and 1974.

The second hypothesis is that heavy dolphin mortality in the 1960's and early 1970's may have somehow affected dolphin pregnancy rates. Large reductions in dolphin mortality occurred following the passage of the Marine Mammal Protection Act of 1972 (Table 9). If mortality rates were higher for nursing calves, calving interval might have been shortened. This would result in higher pregnancy rates and lower lactation rates, both of which were observed in 1971-73. Analyses have indicated that very young calves are more susceptible to tuna-net mortality (Powers and Barlow fn. 3; Stuntz[6]). Indirectly, high calf mortality may also result from the separation of a calf from its mother during long chases. It is not known if the magnitude of these effects could have resulted in the observed changes in pregnancy or lactation rates.

The third hypothesis is that sampling methods were somehow different between 1971-73 and 1974-83. The only difference in the sampling design was that in 1971-73, scientific technicians were placed only on tuna vessels that agreed to cooperate. Beginning in 1974, the selection of vessels was random. It is difficult, however, to see how this change would affect the percent pregnant in the samples. As was noted above, percent pregnant was significantly correlated with sampling season, dolphin kill-per-set, and tuna catch-per-set during the years 1971-73, but not during the years 1974-83. The reason for this difference is not known, but this would seem to be evidence that sampling was more random in the latter period.

The observed change in percent pregnant from 1971-73 to 1974-83 cannot be explained with certainty. The high pregnancy rates in 1971-73 can be logically explained by direct or indirect effects of the fishery or by sampling biases in those years (Hypotheses 2 and 3). Determining whether either (or both) hypothesis is true may not be possible with existing data.

Trends in Percent Lactating

Changes were also found in the percentage of lactating females. For mature females, the fraction lactating shows low values in 1971-73 and high values in 1974-83, which is opposite the pattern seen for fraction pregnant. This inverse correlation would be expected given that pregnancy state and lactation state are physiologically linked (i.e., cessation of lactation leads to ovulation and pregnancy). Perhaps more meaningful is the increase in the fraction of pregnant females that were lactating. Because being simultaneously pregnant and lactating represent the greatest energy drain on female dolphins, this quantity is likely to be very sensitive to changes in environmental conditions. Because nonpregnant females are excluded, this quantity should also be insensitive to sample biases that are related solely to pregnancy state.

TABLE 9.—Estimates of numbers of spotted dolphins killed by all purse seine vessels in the eastern tropical Pacific, 1968-78 (data from Smith 1983).

Year	Spotted dolphins killed
1968	178,000
1969	365,000
1970	355,000
1971	176,000
1972	288,000
1973	131,000
1974	95,000
1975	105,000
1976	47,000
1977	22,000
1978	19,000

Given that no trends were seen in the percent pregnant from 1974 to 1983, we can infer that the calving interval, or the mean period between births for a mature female, also did not change during that time. If calving interval were constant, the increase in the fraction of pregnant females that were lactating indicates that females may be nursing their calves for a longer period of time, hence a longer lactation period. This increase in the lactation period may have resulted from a decrease in fishery related calf mortality during the 1971-83 period. Because calves may be more susceptible to death or separation from their mothers during the chase, capture, and release of a dolphin school, mean lactation periods may have been abbreviated during the earlier years (Hypothesis 2 above).

Trends in Percent Mature

No significant trends in the percentage of females that were sexually mature during 1971-83 are evident for the northern stock of spotted dolphins. Annual variability was far too great to be explained by random sampling error. This parameter showed a significant correlation with dolphin kill-per-set. Therefore, unless sampling conditions remain constant (which they have not), percent mature is not a useful index for monitoring reproductive capability of the spotted dolphin populations.

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[6] Stuntz, W. E. 1980. Variation in age structure of the incidental kill of spotted dolphins, *Stenella attenuata*, in the U.S. tropical purse-seine fishery. Admin. Rep. LJ-80-06, 29 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Variability in percent mature with sampling conditions may result from several interacting factors. Preliminary data have indicated that spotted dolphins in the ETP may segregate on the basis of reproductive maturity (A. A. Hohn fn. 4 and M. D. Scott fn. 5). Schools that consist principally of immature dolphins may have a smaller characteristic school size, may be less likely to have large numbers of tuna associated with them, and may be more vulnerable to high kills-per-set due to the inexperience of younger dolphins. Also, the consistent underrepresentation of immature age classes in the spotted dolphin age distribution (Barlow and Hohn 1984) indicates that a very significant bias may occur in the sampling of immature animals. These are largely speculations, and until a well-supported explanation for sampling variability is presented and until some method of removing this bias is found, percent mature should not be used as an index of changes in spotted dolphin reproduction.

Gross Annual Reproductive Rate

Changes in GARR have been used as a measure of changes in the net rate of growth for a population (Smith 1983). This approach has been faulted on the basis that it does not consider age structure effects (Polacheck 1982), and more critically on the basis that such an approach is theoretically unsound (Goodman[7]). These criticisms do not, however, detract from the usefulness of GARR as an index of gross per capita reproduction for a population.

If GARR were robust to sampling conditions, it could be one of the most useful indices of population reproduction. One advantage is that a GARR index considers percent pregnant and percent mature simultaneously, and hence compensatory changes in these two do not affect the index. Simply stated, GARR is calculated as (the fraction of females in a population) × (the fraction of females that are mature) × (the fraction of mature females that are pregnant)/(gestation time). Unfortunately, percent mature is a major component in these calculations, and this parameter has been found to be dependent on sampling conditions. Until sampling problems associated with estimating percent mature are resolved, GARR is not likely to be a useful index of change in reproductive rates.

Between-Population Comparisons

The northern and southern stocks of spotted dolphins have been subjected to very different levels of fishing-related mortality. Smith[8] has estimated the northern stock to be at 38-55% of its 1959 level and the southern stock to be at 93-98% of its historical level. Density dependent increases in reproductive rates might be predicted for the northern stock relative to the southern stock.

The percentage of mature females that were pregnant differs significantly between the northern and southern stocks. Surprisingly, however, the southern stock was found to have the higher percent pregnant (36% vs. 33%). Another exploited population of spotted dolphins in the western Pacific was found to have an annual pregnancy rate of 0.254 (Kasuya 1976), which (with a gestation time of 11.2 mo) would give an average percent pregnant of about 24%. Considerable variability in percent pregnant can thus exist between spotted dolphin populations, none of which is obviously related to density compensatory effects. Sampling of the southern population has, however, been sporadic, and if annual variability in pregnancy rates is greater for that stock, a few years' data may not be sufficient to accurately estimate a long-term mean. Nonetheless, the tendency for a more exploited stock to have lower reproductive rates is worrisome, and future life history comparisons between the northern and southern stocks would probably be useful.

Evidence for density compensatory changes in pregnancy rates were also lacking when two spinner dolphin, *S. longirostris*, populations were compared (Perrin and Henderson 1984). They found similarly that the more heavily exploited stock (eastern spinners) had a lower percent pregnant than the less heavily exploited stock (whitebelly spinners). The opposite would be predicted based purely on density compensatory effects.

The overall percentage of pregnant females that are lactating is significantly higher for the northern spotted dolphins than for the southern stock. The biological significance of this result is questionable given the year-to-year variability in this parameter. Between-population comparisons of this percentage are not likely to be meaningful until the cause of this large annual variability is identified.

As was noted above, the percentage of females that are mature also appears to be higher in the southern stock than in the northern stock. Given the dependence of this parameter on sampling conditions, little confidence should be placed on this result. The direction of the difference (more immatures in the northern population) is consistent with a higher population growth rate in the north. Work is in progress to determine whether this difference could be due to differences in the age at sexual maturation (Myrick[9]).

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[7] Goodman, D. 1984. Uses of the gross annual reproduction rate calculation in the dolphin assessment. Admin. Rep. LJ-84-22C, 17 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[8] Smith, T. D. (editor). 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). Admin. Rep. LJ-79-41, 120 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

No data exist yet on the mean age at sexual maturation for females in the southern stock. As mentioned in the Methods section, data do exist on the "length at sexual maturation" for both the northern and southern stocks. For the northern stock, this length appears to have increased from 176 cm in 1974 to 181 cm in 1983. For the southern stock this length was estimated as 175 cm from the pooled 1974-83 data. The length at sexual maturation is greater for the northern stock, which is consistent with the greater mean asymptotic length of the northern specimens (Perrin et al. 1979).

CONCLUSION

My intent in writing this paper was to identify indices that may be of value in monitoring the reproductive health of spotted dolphins in the eastern Pacific. Two of the indices that were examined (the percentage of mature females that are pregnant and the percentage of pregnant females that are lactating) are likely to be useful for this purpose. Both are relatively insensitive to sampling biases, and both measure important aspects of the female reproductive cycle. Problems exist in measuring the fraction of females that are mature. This parameter is also an important index of net reproduction in a population. It is possible that a stable index of percent mature could be obtained using some stratification scheme. A first approach might be to examine finer scale geographic differences in percent mature. Additional work is necessary before significance can be ascribed to between-population differences in percent mature.

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LITERATURE CITED

Barlow, J., and A. A. Hohn.
1984. Interpreting spotted dolphin age distributions. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-NMFS-SWFC-48, 22 p.

Dixon, W. J. (editor).
1981. BMDP statistical software. Univ. Calif. Press, Berkeley, 725 p.

Fowler, C. W.
1984. Density dependence in cetacean populations. Rep. Int. Whaling Comm., Spec. Issue 6:373-379.

Gambel, R.
1975. Variations in reproduction parameters associated with whale stock sizes. Rep. Int. Whaling Comm. 25:182-189.

Hester, R.
1984. Possible biases in the estimates of rates of reproduction in the spotted dolphins, *Stenella attenuata*. Rep. Int. Whaling Comm., Spec. Issue 6:337-341.

Kasuya, T.
1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Sci. Rep. Whales Res. Inst. 28:73-106.

Laws, R. M.
1956. Growth and sexual maturity in aquatic mammals. Nature (Lond.) 178:193-194.

Lockyer, C. H.
1972. The age of sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug. J. Cons. Int. Explor. Mer 34:276-294.

Mizroch, S. A.
1983. Reproductive rates in Southern Hemisphere baleen whales. MS Thesis, Univ. Washington, Seattle, 103 p.

Myrick, A. C, Jr., A. A. Hohn, J. Barlow, and P. A. Sloan.
In press. Reproduction in the female spotted dolphin, *Stenella attenuata*. Fish. Bull., U.S.

Perrin, W. F.
1970. Color patterns of the eastern Pacific spotted porpoise *Stenella graffmani* Lönnberg (Cetacea, Delphinidae). Zoologica (N.Y.) 54:135-149.

Perrin, W. F., J. M. Coe, and J. R. Zweifel.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

Perrin, W. F., and J. R. Henderson.
1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitations. Rep. Int. Whaling Comm., Spec. Issue 6:417-430.

Perrin, W. F., R. B. Miller, and P. A. Sloan.
1977. Reproductive parameters of the offshore spotted dolphin, a geographic form of *Stenella attenuata*, in the eastern tropical Pacific, 1973-75. Fish. Bull., U.S. 75:629-633.

---

[9] A. C. Myrick, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1984.

PERRIN, W. F., P. A. SLOAN, AND J. R. HENDERSON.
1979. Taxonomic status of the "southwestern stocks" of spinner dolphins, *Stenella longirostris*, and spotted dolphins, *S. attenuata*. Rep. Int. Whaling Comm. 29:175-184.

POLACHECK, T.
1982. The relationship between changes in gross reproductive rate and the current rate of increase for some simple age structured models. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-19, 9 p.

RASMUSSON, E. M., AND T. H. CARPENTER.
1982. Variations in tropical sea surface temperature and surface wind fields associated with the Southern Oscillation/El Niño. Mon. Weather Rev. 110:354-384.

SMITH, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eatern tropical Pacific. Fish. Bull., U.S. 81:1-13.

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A production model analysis of the North Pacific albacore population including estimates of the sensitivity of results to measurement errors in input data

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Abstract

A production model analysis is done for a single stock of North Pacific albacore using total catch and standardized fishing effort data. A sensitivity analysis using a Monte-Carlo simulation is done to estimate the sensitivity of predicted results to errors in both catch and effort data. Results indicate that best fitting estimates of Maximum Sustainable Yield (MSY) are robust with respect to errors in input data of up to plus or minus 20% and range for 71,000 to 108,000 tons. Further, it is shown that errors in catch and effort have relativly independent effects on the predicted results. Effects of assumptions underlying the production model analysis are discussed.

Background

The North Pacific albacore resource has been fished since the turn of the century by Japanese and United States fishermen. Early records indicate landings in the United States were in the 7,000 to 13,000 tons range from 1916 to 1925, near zero between 1926 and 1937, and again in the 5,000 to 10,000 tons range from 1938 through 1947 (CLEMENS and CRAIG, 1965). Available records for the Japanese albacore fishery indicate that a fishery for albacore existed since about the turn of the century, with catches during the 1927 to 1936 period ranging from about 8,000 to 18,000 tons and averaging about 12,000 tons (AIKAWA, 1949). From 1936 through 1946, Japanese catches were low. Following 1946 landings by both Japanese and United States fishermen increased rapidly. In the early 1950's Japanese landings were in the 50,000 to 68,000 tons range and United States landings ranged from 16,000 to 26,000 tons. Landings have remained high to the present.

Although catch data for a long period of time exists, only recently, since 1961, has relatively complete data on fishing effort been collected for both Japanese and United States fisheries. To help assess the overall condition of tuna stocks the generalized production model along with other evidence can be used. The production model affords a useful estimate of the

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relation between expected equilibrium catch and exploitation rate or fishing effort (SCHAEFER, 1954, 1957; FOX, 1975).

This analysis applies the generalized production model to North Pacific albacore data from 1961 to 1981. Additionally, a sensitivity analysis is performed to determine how the model results behave with respect to various levels of random error in the input catch and effort data.

Data and Preparation

Data on catch and effort used here are shown in Table 1. These data were taken from a working document by SHIOHAMA as reported in the Report of the Eighth North Pacific Albacore Workshop (BARTOO and KUME, 1984) and are considered to be essentially complete and correct for the time period concerned.

The standardization of effort among the longline, pole-and-line and troll gears was done by the method of SHIOHAMA (1979) which is essentially the same as used by COAN and FOX (1977) for Atlantic yellowfin tuna. Within each gear, the time series of CPUE values is scaled so that the mean CPUE has a value of 1.0; this is standardized CPUE (Table 1). Standardized effort is calculated by dividing the catch in tons by the appropriate standardized CPUE. This is done by gear and year. Total standardized effort for each year is the sum of the standardized effort for each gear (Table 1).

Table 1. Annual yield in tons, CPUE and standardized effort for the North Pacific albacore, 1961-1981.

Year	CPUE (d_{lk})			Standardized CPUE (S_{lk})			Catch in tons (W_{lk})				Standardized effort (E_{lk})				Number of age
	Pole-and-line	Long-line	U.S.A. Surface	Pole-and line	Long-line	U.S.A. Surface	Pole-and-line	Long-line	U.S.A. Surface	Total	Pole-and-line	Long-line	U.S.A. Surface	Total	
1961	4.40	0.25	69.17	0.80	0.78	0.75	18,636	17,437	16,250	52,323	23,295	22,355	21,667	67,317	4
1962	7.22	0.30	124.59	1.31	0.94	1.36	8,729	15,764	22,520	47,013	6,663	16,770	16,559	39,992	4
1963	6.29	0.32	132.09	1.14	1.00	1.44	26,420	13,464	28,740	68,624	23,175	13,464	19,958	56,597	4
1964	6.86	0.40	97.61	1.25	1.25	1.06	23,858	15,450	22,627	61,943	19,086	12,366	21,346	52,798	4
1965	6.26	0.33	89.07	1.14	1.03	0.97	41,491	13,701	17,624	72,816	36,396	13,302	18,169	67,867	4
1966	5.94	0.54	90.45	1.08	1.69	0.98	22,830	25,050	17,401	65,281	21,139	14,822	17,756	53,717	4
1967	6.09	0.40	126.83	1.11	1.25	1.38	30,481	28,869	22,795	82,145	27,460	23,095	16,518	67,073	4
1968	5.34	0.38	135.23	0.97	1.19	1.47	16,597	23,961	27,326	67,884	17,110	20,135	18,589	55,834	4
1969	4.95	0.28	112.57	0.90	0.88	1.23	32,107	18,006	23,545	73,658	35,674	20,461	19,142	75,277	4
1970	6.13	0.31	127.39	1.11	0.97	1.39	24,376	15,372	26,631	66,379	21,960	15,847	19,159	56,966	4
1971	6.94	0.21	96.68	1.26	0.66	1.05	53,198	10,915	27,029	91,142	42,221	16,538	25,742	84,501	4
1972	6.25	0.30	61.08	1.13	0.94	0.66	60,762	12,622	31,545	104,929	53,772	13,428	47,795	114,995	4
1973	5.49	0.38	82.89	1.00	1.19	0.90	69,811	16,000	19,246	105,057	69,811	13,445	21,384	104,640	4
1974	7.81	0.34	105.17	1.42	1.06	1.15	73,576	12,952	26,900	113,428	51,814	12,219	23,391	87,424	4
1975	5.98	0.23	99.81	1.09	0.72	1.09	52,157	9,931	23,513	85,601	47,850	13,793	21,572	83,215	4
1976	6.13	0.30	69.22	1.11	0.94	0.75	85,336	15,738	20,032	121,106	76,879	16,743	26,709	120,331	4
1977	3.01	0.26	59.90	0.55	0.81	0.65	31,934	15,512	12,181	59,627	58,062	19,151	18,740	95,953	4
1978	3.58	0.23	86.80	0.65	0.72	0.95	59,877	12,888	17,535	90,300	92,118	17,900	18,458	128,476	4
1979	3.50	0.24	45.41	0.64	0.75	0.49	44,662	14,174	6,920	65,756	69,784	18,899	14,122	102,805	4
1980	4.44	0.33	36.78	0.81	1.03	0.40	46,743	14,660	8,367	69,770	57,707	14,233	20,918	92,858	4
1981	3.05	0.31	80.11	0.55	0.97	0.87	27,426	17,876	16,038	61,340	49,865	18,429	18,434	86,728	4
Σd_{lk}	115.66	6.64	1928.85												
$\bar{d}$	5.51	0.32	91.85												

Results of production modeling and sensitivity analysis

The data series described previously was used as input data for the generalized production model (FOX, 1975). Additionally, a Monte-Carlo sensitivity analysis was done to estimate the expected changes in results of the model due to errors in the data.

The results of the production model analysis ara similar to those presented by SHIOHAMA (MS.). Under various forms of the model, m (shape parameter)$=0.0$, 1.0, and 2.0, predicted MSY values are 136,000 tons, 87,000 tons and 86,000 tons respectively. These were obtained without weighting, averaging four significant ages in the catches. The goodness of fit ranged from 50% to 56%. The best fit case was approximately $m=1.1$ (in the interval 1.00-1.09). The predicted MSY was 89,000 tons (Fig. 1). Equilibrium effort associated with MSY, FOPT (optimum effort), is predicted to be 134,000 units, approximately the level reached in 1976.

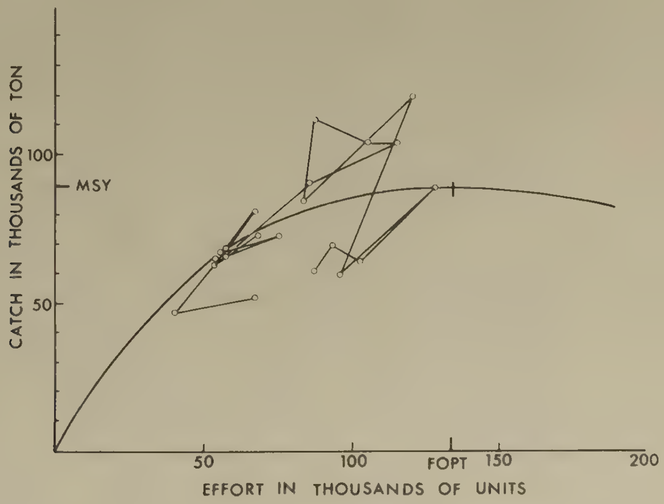

Fig. 1. Results of best fitting generalized production model fitted to North Pacific albacore data. Maximum sustainable yield (MSY) and associated effort (FOPT) are shown.

A sensitivity analysis was performed to determine the expected range of MSY and FOPT given various levels of error in the data. The method is the same as used by BARTOO and COAN (1983) for Atlantic albacore. The Monte-Carlo analysis generated new sets of data to be fitted by the production model. Each new set of data contained catch and effort data corresponding exactly to the actual annual data points values. However, the actual value of each new data point was allowed to vary; this represented the uncertainty of inaccuracy in the original data. Each new point was allowed to vary uniformly about the actual data point + or − some chosen percentage, X. For example, if the actual catch was 20,000 tons and the uncertainty level was +

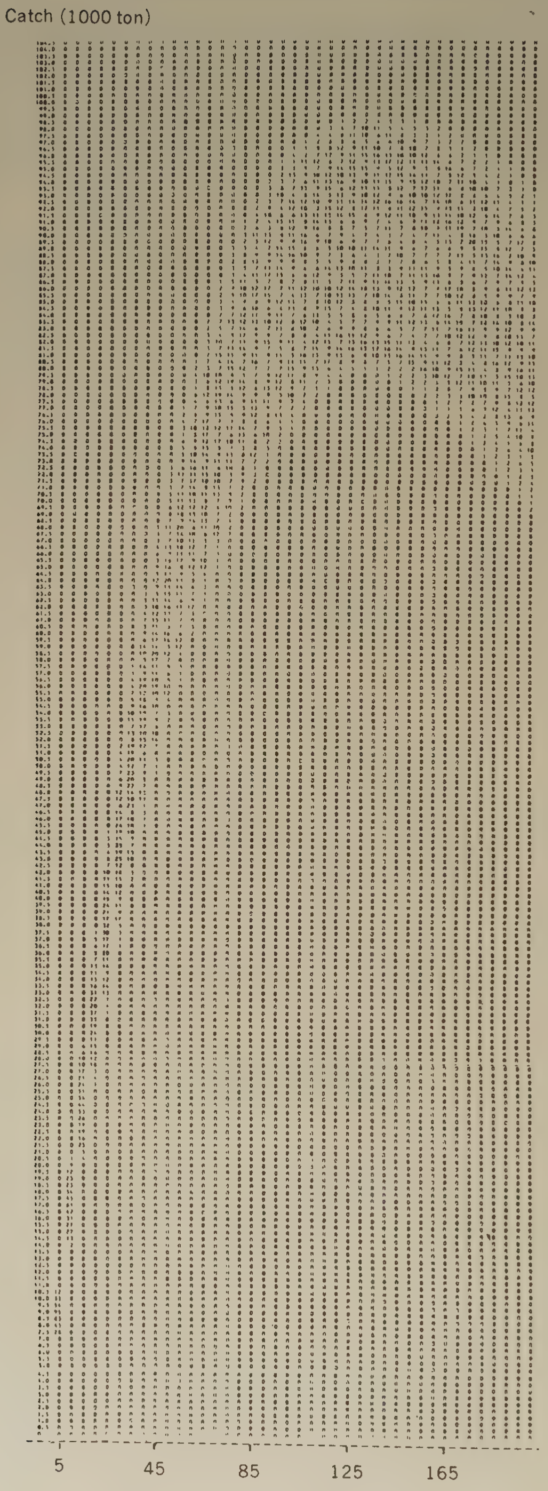

Fig. 2. Distribution of results from Monte-Carlo simulation (see text) with errors in both catch and effort of up to + or − 10 %. Number of simulated data cases=350.

or −10%, each new generated data point could vary between 18,000 and 22,000 tons with all values in this range equally probable.

Each set of data was fitted to the production model and the results saved. This was done 300 times or more for each particular combination of error level. An example of the results is shown in Fig. 2. This is the distribution of results for the case of an assumed error in both catch and error of up to + or −10%.

For all levels of error (up to 20%) in catch, effort, or catch and effort the best fitting model *m* was in the 1.0 to 1.09 range, indicating that with this data set the shape of the model is not likely to change until additional data have been added to the series which deviates from the current trends. The "goodness-of-fit" for all cases was about 50%. This, however, may not be a meaningful measure which can be directly correlated to "confidence" in the results. A good measure of confidence is the range of expected results at different error levels.

Shown in Fig. 3 are the distributions of 99% of the MSY values for varying levels of error in catch, effort or catch and effort. As can be readily seen in Fig. 2 the range of MSY values is very insensitive to errors in effort. However, MSY is sensitive to errors in catch. A + or −20% error in catch causes MSY to vary from +21% to −20% (an asymmetric distribution). For the case of errors in both catch and effort the results are almost identical to the case of catch error alone.

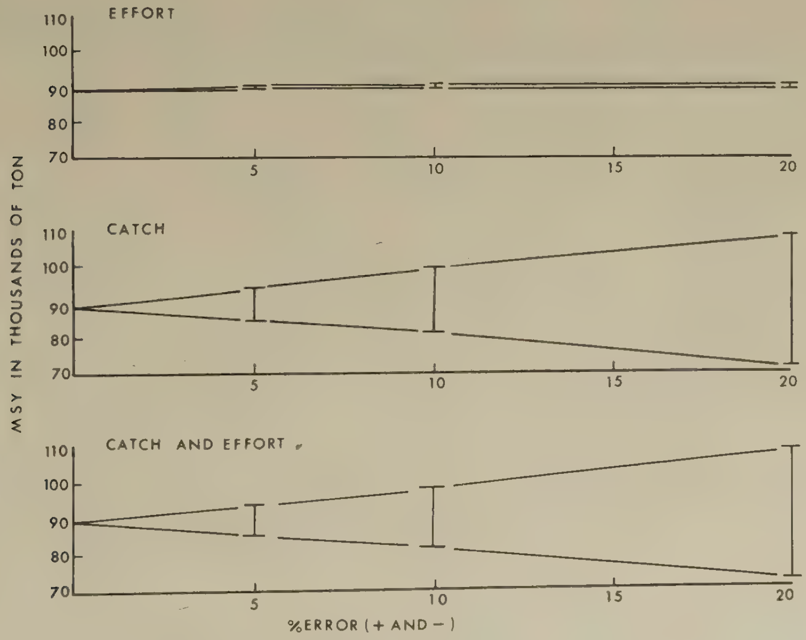

Fig. 3. Results of North Pacific albacore production model sensitivity analysis showing the predicted range of MSY values for various lavels of error in the input data.

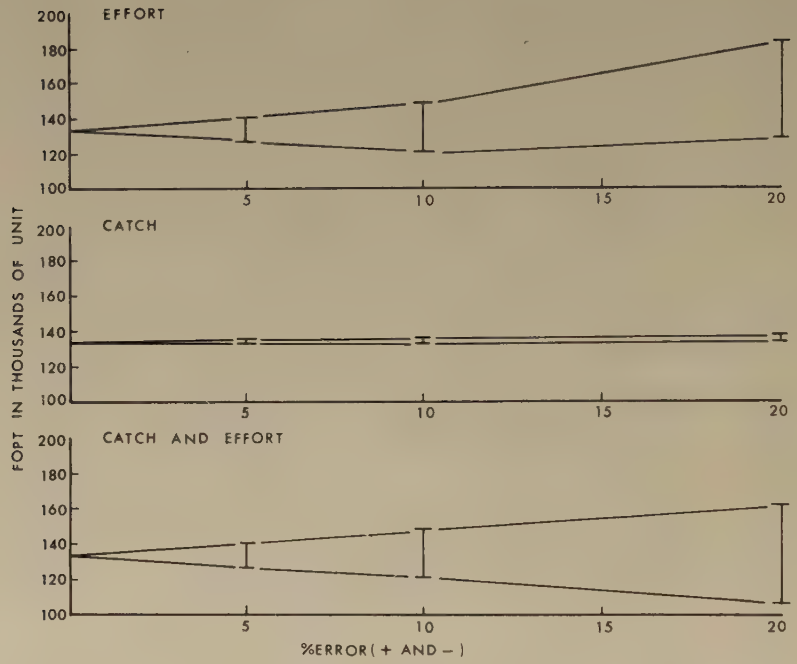

Fig. 4. Results of North Pacific albacore production model sensitivity analysis showing the predicted range of FOPT values for lerious vavels of error in the input data.

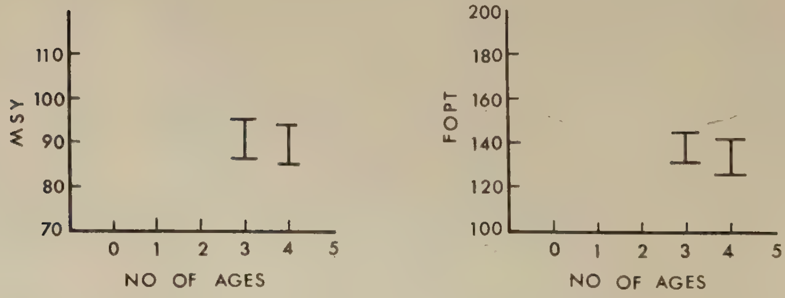

Fig. 5. Results of North Pacific albacore production model sensitivity analysis showing the predicted range of MSY values and FOPT values as functions of number of ages assumed significant in the catch (see text).

Fig. 4 shows the distributions of 99% of the FOPT values for varying levels of error in catch, effort or catch and effort. The range of FOPT associated with different levels of catch error is quite narrow. FOPT is not sensitive to errors in the catch. FOPT is sensitive to errors in effort. Errors on the order of + to −20% cause FOPT to vary +35% to −5%, with a slightly skewed distribution. Errors in catch and effort of + and −20% generate a range of FOPT values of +21% to −20%, not nearly as skewed as in the case of effort error alone.

The effect of changing the number of ages averaged in the calculations is shown in Fig. 5. The expected ranges for MSY and FOPT are the same using 3 or 4 years smoothing. The mean of the ranges shifts upward somewhat as the number of years goes down.

Conclusions

Results from the deterministic fitting of the production model to the data indicate a range of MSY values of 86,000 to 136,000 tons with a most likely MSY of 89,000 tons ($m=1.1$). This range of values is not greatly different from the values reported previously (BARTOO and KUME, 1984), although the most likely MSY value is slightly lower than the previously estimated. Some of these changes are due to fitting the model without weighting the recent data heavier than earlier data (*i.e.* assuming that the whole data series is of good quality). From the results of the sensitivity analysis it appears that the most likely fitting form of the model, $m=1.1$, is relatively robust. Even with large errors in the input data the best fitting model was always close to $m=1.1$. In another analysis on Atlantic albacore (BARTOO and COAN, 1983) noted that with moderate errors assumed in the input data the distribution of the best fitting models included several values of m, as different as $m=0.5$ and $m=1.0$. We therefore conclude that with the given data and their treatment the $m=1.1$ model is quite robust and is not likely to change without a marked change in the data or their treatment.

The actual value of MSY is less sure. The point estimate is 89,000 tons. However, as seen in the results of the sensitivity analysis random errors in the catch data cause a range of expected MSY values. A possible range of error in the measurement of total catch of up to + or − 20% produces a range of MSY values from 71,000 to 108,000 tons. Errors in the estimation of fishing effort have little or no effect on the range of MSY estimates.

The effort level associated with MSY, FOPT, is estimated to be 134,000 units, approximately the level reached in 1976 when a peak catch of 121,106 tons was taken. Effort in 1981 is estimated at 87,000 units, almost 30% lower than FOPT. The sensitivity analysis results show that a range of FOPT estimates result from assumed errors in the effort data. An error range of up to + or −20% gives a range of FOPT values of 107,000 units to 162,000 units. Errors in catch data have little or no effect on the estimation of FOPT.

If the number of ages assumed to be significantly contributing to the catch is reduced to 3 from 4, the range on both MSY and FOPT shifts upward in value about 2%. This is due to reduced smoothing of the data. This increases the likely range of MSY values from 71,000 to 110,000 tons.

The application of the generalized production model to fisheries data requires several assumptions, some of which may not be fully met in the case of North Pacific albacore. Among the most critical assumptions is the assumption that the catchability coefficient, q, has been subjected to only random variability. Further, when effort of the several gears is standardized and combined, the average values for q are assumed equal for the various gears. In the case of North Pacific albacore we cannot verify that these assumptions are fully met. This is the same for most applications of the production model. However, in the case of North Pacific albacore the relative level of the catches made by each of the fishing gears has remained approximately the same for the time period under study. This should have the effect of making any absolute bias in the estimation of fishing effort more or less constant, preserving the underlying trends. The results of the sensitivity analysis suggest that the estimates of MSY are robust with respect to errors in effort. Therefore, barring systematic changes in q, the current estimates of MSY appear reasonable and may be considered as accurate as others calculated for other tuna stocks.

References

相川広秋 1949 : 水産資源学総論. 456 (545pp). 産業図書. 東京. (AIKAWA, H. 1949 : An introduction to fisheries population dynamics. 456 (545pp). Sangyotosho. Tokyo.)

BARTOO, N. and A. COAN 1983 : Production model analysis of the South Atlantic albacore stock and effects of data accuracy (SCRS/82/52). ICCAT Col. Vol. Sci. Pap., Vol. (2), 421-433.

BARTOO, N. and S. KUME 1984 : Report of the Eighth North Pacific Albacore Workshop. In Press (in Japanese and English).

CLEMENS, H. B. and W. L. CRAIG 1965 : An analysis of California s albacore fishery. California Department of Fish and Game, Fish Bull., (128), 302pp.

COAN, A. and W. W. FOX 1977 : A Production model analysis of the status of yellowfin tuna in the Atlantic Ocean, 1964-1975 (SCRS/76/70). ICCAT Col. Vol. Sci. Pap., Vol. (1), 124-313.

FOX, W. W. 1975 : Fitting the generalized stock production model by least-squares and equilibrium approximation. U. S. Fish. Bull., Vol. 73 (1), 23-36.

LENARZ, W. H. and W. W. FOX 1974 : Production model analysis of Atlantic yellowfin tuna fishery, 1964-1973 (SCRS/74/32). ICCAT.

LENARZ, W. H. and A. COAN 1975 : Assessment of the Condition of the North Atlantic albacore fishery (SCRS/74/31). ICCAT Col. Vol. Sci. Pap., Vol. IV, 76-88.

SCHAEFER, M. B. 1954 : Some aspects of the dynamics of populations important to the management of commercial marine fishes. Inter-Am. Trop. Tuna Comm., Bull. (1), 25-56.

——— 1957 : A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. (2), 245-285.

SHIOHAMA, T. 1977 : Stock assessment of Atlantic albacore by production model analysis (SCRS/76/31). ICCAT Col. Vol. Sci. Pap., Vol. VI (2), 233-236.

——— 1979 : Stock assessment of the North Pacific albacore by production model analysis. Working paper for the Third North Pacific Albacore Workshop, NPALB/78/1, 8pp.

入力データーの誤差が推定値に与える影響を考慮した北太平洋ビンナガのプロダクションモデル解析

Norman BARTOO・塩浜利夫

摘　　要

漁獲量および標準化した漁獲努力量データーを用いて，プロダクションモデルにより，北太平洋ビンナガの資源解析を行った。さらに，モンテカルロシュミレーションを用いた感度分析により，漁獲量と努力量に与えた誤差に対する期待値の感度を推定した。最大持続生産量（MSY）の最適推定値は±20％までのモデル入力データーの誤差に対しても安定しており，71,000〜108,000トンの範囲を示した。また，漁獲量と努力量に誤差を与えた場合でも比較的独立した形で推定値に影響を与えることが示された。プロダクションモデルの適用に際して前提条件の結果に与える影響を論議した。

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ACUTE TOXICITY OF SEVEN ALICYCLIC HEXANES TO STRIPED BASS, *MORONE SAXATILIS,* AND BAY SHRIMP, *CRANGON FRANCISCORUM,* IN SEAWATER [1]

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Field monitoring studies have shown that many striped bass, *Morone saxatilis,* in California's Sacramento-San Joaquin Estuary are burdened with a wide variety of pollutants including many types of petroleum hydrocarbons. Alicyclic hydrocarbons are among these pollutants but there was no information on their toxicity to striped bass. Our studies were concerned with the acute toxicities of the simplest alicyclics in comparison to their counterparts in the aromatic series. The alicyclic compounds were cyclohexane, methylcyclohexane, ethylcyclohexane and four dimethylcyclohexanes (1,1; 1,2; 1,3; and 1,4). Acute toxicities after 24 and 96 h exposures to seven alicyclic hexanes were determined for striped bass and one of their major food organisms, the bay shrimp, *Crangon franciscorum.* The 96 h LC_{50}s for striped bass and bay shrimp ranged from 3.2 to 9.3μl/l and from 1.0 to 6.2 μl/l, respectively. Slight differences were noted between the 24 and 96 h LC_{50} values in all but two bioassays. Solubilities of these alicyclics in seawater and freshwater were determined since information in the literature was limited. Solubility was inversely related to the complexity of the alicyclic structure and ranged from 5.3 to 62 μl/l in distilled water and from 4.6 to 44 μl/l in seawater. Alicyclics were generally more soluble in distilled water than in seawater. Tissue analyses showed greater bioaccumulation in striped bass, which have more lipid than bay shrimp. Striped bass had up to 260 μl/kg (wet weight) of an alicyclic hexane after exposure to water concentrations ranging from 0.32 to 12 μl/l. Bay shrimp residues were as much as 110 μl/kg of an alicyclic hexane.

INTRODUCTION

Alicyclic hexanes were recently found in liver and ovary tissues (0.02 to 16 μl/kg wet weight) of striped bass, *Morone saxatilis,* taken from the Sacramento-San Joaquin Estuary (Whipple, Eldridge and Benville 1981). Along with monocyclic aromatic hydrocarbons, the alicyclics were associated with poor physiological conditions (egg resorption and lesions with cestode larvae) leading to possible organ dysfunctions. Because little information exists on the toxic effects of these petroleum compounds, we conducted a series of experiments to determine the toxicological consequences of alicyclic hexanes to striped bass and bay shrimp, *Crangon franciscorum.*

Alicyclic hexanes are six-carbon ring structures in the cyclic aliphatic hydrocarbon class (cycloalkanes) of organic compounds which are relatively nonpolar and have low solubility in water (Morrison and Boyd 1966). Seven low molecular weight alicyclic hexanes found in the tissues of striped bass collected from the San Francisco Bay were selected for acute toxicity tests. These alicyclics were: cyclohexane, methylcyclohexane, four dimethylated forms 1,1-; cis- and trans-1,2—; cis-1,3—; and cis- and trans-1,4-dimethylcyclohexane (DMCH), and ethylcyclohexane (ECH) (Figure 1).

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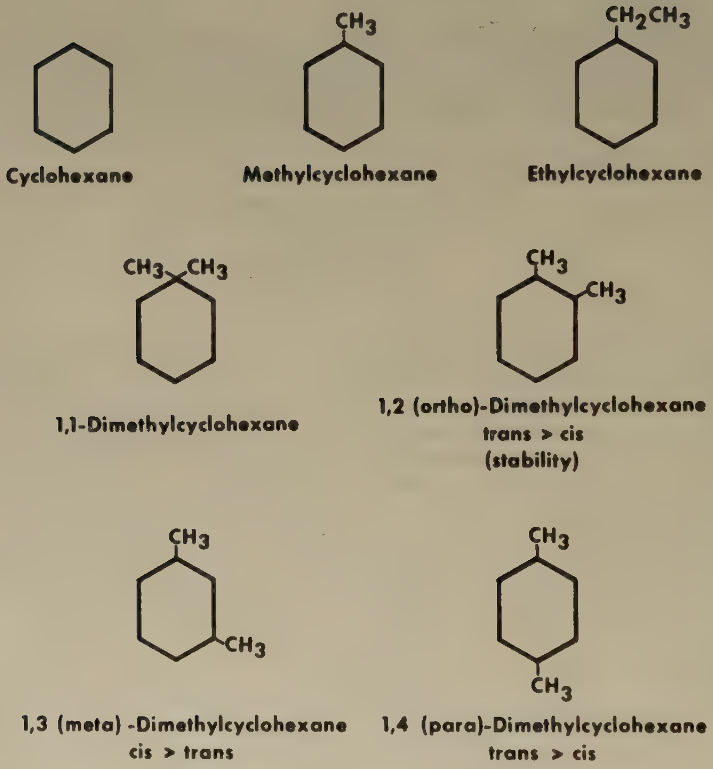
CH3
CH2CH3
Cyclohexane
Methylcyclohexane
Ethylcyclohexane
CH3 CH3
CH3
CH3
1,1-Dimethylcyclohexane
1,2 (ortho)-Dimethylcyclohexane
trans > cis
(stability)
CH3
CH3
CH3
CH3
1,3 (meta) -Dimethylcyclohexane
cis > trans
1,4 (para)-Dimethylcyclohexane
trans > cis

FIGURE 1. Structural formulas of seven alicyclic hexanes.

While some alicyclics entering the aquatic environment are of biogenic origin (e.g. plant metabolites), most alicyclics are from anthropogenic sources such as oil spills and waste discharges.

MATERIALS AND METHODS

Solubility Determinations

The lack of published solubility values for most of the seven alicyclics necessitated the determination of their solubility in distilled water and seawater before we could conduct the toxicity experiments.

To determine the solubilities of the seven alicyclics, saturated solutions were prepared by shaking 0.22 ml of each alicyclic with 220 ml water in a 250 ml separatory funnel for 1 min and letting the mixture settle for 24 h at 20° C. Two 100 ml portions of the saturated water extracts were drained into 125 ml separatory funnels; each portion was extracted in succession with three 10 ml aliquots of TF-Freon (trichlorotrifluoroethane) (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.). Samples were processed as described under Analytical Procedure, below.

Bioassay Procedure

Juvenile striped bass (mean weight = 8.5 g, mean total length = 9.2 cm) were obtained from freshwater at the U.S. Bureau of Reclamation fish screening facility at Tracy, California, and acclimated to seawater at our laboratory in Tiburon, California. Bay shrimp (mean weight = 1.7 g, mean length = 6.4 cm), were acquired from a local bait dealer in San Rafael, California. Mortality from transportation and salinity change during the first 24 h was 20% for striped bass and less than 1% for bay shrimp. All animals were held in flow-through 200 l tanks for 2 wk before toxicity testing (Korn 1975). Mortality during this period was less than 1% for both fish and shrimp. Salinity and temperature of the seawater increased during the holding period from 27 to 32 °/₀₀ and 15 to 20°C, respectively.

Static bioassays were conducted with each alicyclic using five oval fiberglass aquaria with dimensions of 110 cm length × 50 cm width × 40 cm height. Each aquarium was filled with 180 l of filtered seawater. Five alicyclic aliquots ranging in geometric progressions from 1 to 16 ml were mixed with seawater to achieve the necessary nominal concentrations. Test-tank solutions were prepared by adding the alicyclics slowly (8 ml/min) into a mechanically-generated seawater vortex. Immediately after the appropriate amount of alicyclic was introduced into each aquarium, ten animals of each species were placed in each aquarium. No aeration was used during the testing period. The bay shrimp were separated from the fish by placing them in a 30 cm length × 16 cm width × 14 cm height basket. Two 10 ml seawater samples were pipetted at mid-depth from each aquaria before and after introducing the animals to determine the alicyclic concentrations. These samples were immediately extracted with 10 ml of TF-Freon and analyzed as described under Analytical Procedure. Each succeeding day a 100 ml water sample was taken, extracted and analyzed. Mortalities were noted daily. Bioassay procedures followed were from Standard Methods (Connors, Jenkins and Greenberg 1981). LC_{50}s and confidence limits were calculated by the Litchfield and Wilcoxon (1949) method.

All fish and shrimp were analyzed for alicyclic residues at the end of the 96 h tests. Animals were frozen using dry ice and ground into a powder (Benville and Tindle 1970). A composite of 10 g homogenized tissue was then processed for alicyclic concentrations (Nunes and Benville 1979).

Analytical Procedure

The alicyclics in each Freon extract were separated and analyzed with a Hewlett-Packard 5880 gas chromatograph (GC) equipped with a dual flame ionization detector. Standard solutions of each alicyclic hexane were made for calibrating the GC. A combined standard was made from the seven alicyclics, six monocyclic aromatics and nonane to determine the relative location of each compound (Figure 2). The six aromatics were benzene, toluene, ethylbenzene and three xylene isomers (ortho-, meta, and para-). All alicyclics were eluted from the Bentone-34/SP-1200 column at 65°C within 8 min. After all the alicyclics were separated, the temperature was increased to 120° C to remove all the aromatics. There were overlapping retention times between the DMCHs and ethylcyclohexane (ECH) using the Bentone-34/SP-1200 column. However, each bioassay involved only a single alicyclic and analytical interferences were not encountered. Benzene was eluted within the alicyclic group but caused no interference. Temperature programming was started after 10 min. running time to elute the ethylbenzene and xylene isomers within a reasonable time frame (15 min). The four dimethylated alicyclics and ethylcyclohexane had overlapping retention times and emerged in the following three groups: 1,1-DMCH, *cis*-1,3-DMCH and *trans*-1,4-DMCH; *trans*-1,2-DMCH and *cis*-1,4-DMCH; and *cis*-1,2-DMCH and ECH. No *trans*-1,3-DMCH was available for standardization; consequently its elution time was unknown. One unknown peak appeared at 2.653 min which was an inherent characteristic of the TF-Freon solvent. The ratio of the *cis*- and *trans*-isomers that appeared for 1,2-, 1,3- and 1-4-DMCH were 41/59, 100/0 and 25/75, respectively. Alicyclic data reported in ppm are in µl/l for water sample and µl/kg for tissue samples based on wet weight.

RESULTS

Solubilities

All seven alicyclics had solubilities in the low ppm range (Table 1). The number of alkyl groups on the cyclohexane compounds is in inverse proportion to its water solubility, with cyclohexane the most soluble and dimethyl and ethyl alicyclics the least soluble. In general, the position of the methyl groups appears to affect the solubility. The further apart the two groups were from each other, the less soluble was the DMCH. Solubilities also changed with salinity. Alicyclics, except for ECH, were more soluble in distilled water than in seawater; ECH had the same solubility in both distilled water and seawater. Solubility values ranged from 5.3 to 62 ppm in distilled water and from 4.6 to 44 ppm in seawater. The solubility of most of the alicyclics in seawater was lower by 24 to 29%; *cis*-1,3-DMCH had only a 10% reduction and there was no change for ECH. Ratios of the two optical isomers (*cis*- and *trans*-) in 1,2- and 1,4-DMCH compounds were altered slightly favoring the *cis*- form after they were dissolved in water, from 41/59 and 25/75 to 45/55 and 30/70 for distilled water and 44/56 and 28/72 for seawater, respectively.

Acute Toxicity and Tissue Residues

The alicyclics were more toxic to bay shrimp than to striped bass (Table 2). Acute toxicities of the seven alicyclics ranged from 4.7 to 10.9 ppm for striped bass and from 1.5 to 6.5 ppm for bay shrimp within a 24 h period. The 96 h tests showed slightly higher toxicities, although cyclohexane for striped bass and 1,3-DMCH for bay shrimp had similar acute toxicities for both exposure periods. Mixtures of the *cis*- and *trans*-DMCH (1,2- and 1,4-) isomers were more toxic to both striped bass and bay shrimp than the two pure DMCH's (1,1- and 1,3-). Acute toxicity values (LC_{50}s) of ECH, 1,3-DMCH and 1,4-DMCH for striped bass exceeded the solubility of the compound in seawater; for bay shrimp, only the LC_{50} for ECH and 1,3-DMCH exceeded the seawater solubility.

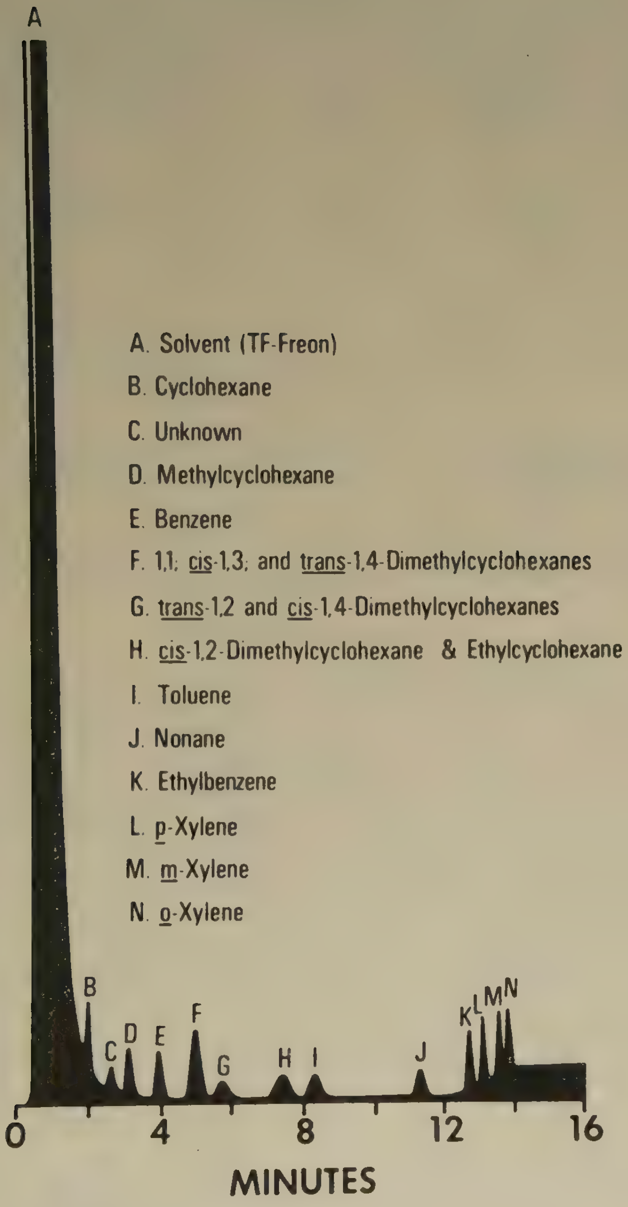

FIGURE 2. Chromatogram of nine alicyclics, six aromatics and nonane.

The striped bass and bay shrimp rapidly bioaccumulated the alicyclics many times above the initial water dosage. Test concentrations of alicyclics in seawater ranged from 0.32 to 11 ppm which resulted in uptakes by striped bass from "nondetectable" levels to 260 ppm (wet weight) and by bay shrimp from 4.4 to 110 ppm (Table 3). Water insoluble alicyclics were accumulated to higher levels by the organisms than were the more soluble ones.

TABLE 1. Physical Properties of the Alicyclic Hexanes.

Compounds	*% Purity*	*Solubility (ppm) @ 20°C* Distilled (cis-/trans-)	*Solubility (ppm) @ 20°C* Seawater (cis-/trans-)	*% Optical Form ** Cis-	*% Optical Form ** Trans-	*Molecular weight*	*Boiling point (C)*	*Density (g/ml)*	*Vapor † pressure (mm Hg)*
Cyclohexane	99+	62	44	—	—	84.16	81	.77	78
Methylcyclohexane	99	18	13	—	—	98.19	101	.77	36
Ethylcyclohexane	99+	5.3	5.3	—	—	112.22	103–132	.778	10
1,1-Dimethylcyclohexane	97	10	7.6	—	—	112.22	118–120	.777	17
1,2-Dimethylcyclohexane	98	8.2(3.7/4.5)	6.1(2.7/3.4)	41	59	112.22	124	.778	11 (*cis-*)
1,3-Dimethylcyclohexane	99	6.2	5.6	100	0	112.22	120	.784	16 (*cis-*)
1,4-Dimethylcyclohexane	98	6.4(1.9/4.5)	4.6(1.3/3.3)	25	75	112.22	120	.773	14 (*cis-*)

* Analyzed by gas chromatography (not corrected for purity).
† Values were calculated for 20°C using Antoine equation in Lange's Handbook of Chemistry (Dean 1979).

TABLE 2. Acute Toxicity of Seven Alicyclic Hexanes to Striped Bass and Bay Shrimp.

	Striped Bass				*Bay Shrimp*			
	24-h		*96-h*		*24-h*		*96-h*	
*Alicyclic Hexanes **	*LC_{50}*	*95%C.L.*	*LC_{50}*	*95%C.L.*	*LC_{50}*	*95%C.L.*	*LC_{50}*	*95%C.L.*
Cyclohexane	8.3	—†	8.3	—	3.4	—	2.4	1.7 - 3.5
Methylcyclohexane	7.0	5.7– 8.6	5.8	—	3.5	3.0 - 4.0	3.3	2.9 - 3.9
Ethylcyclohexane	10.9	6.6–17.5	8.8	6.0–13.0	3.7	2.9 - 4.8	3.1	2.1 - 4.5
1,1-Dimethylcyclohexane	7.5	6.6– 8.5	6.9	6.3– 7.6	6.5	6.1 - 6.9	5.2	—
1,2 Dimethylcyclohexane	4.7	3.2– 6.9	3.2	—	1.5	0.82– 2.6	1.0	0.58 –1.8
1,3 Dimethylcyclohexane	9.9	8.3–11.8	9.3	8.0–10.8	6.2	5.5 - 6.9	6.2	5.5 - 6.9
1,4 Dimethylcyclohexane	6.7	6.0– 7.3	6.5	5.7– 7.3	2.8	2.0 - 3.8	1.5	—

* 1,2 and 1,4 dimethylcyclohexanes are mixtures of cis and trans isomers.
† No confidence limits were calculated from bioassays without partial mortalities.

TABLE 3. Resulting Concentrations of Alicyclic Hexanes in Tissues of Striped Bass and Bay Shrimp from Test Containers.

	Concentration Range of Alicyclics (ppm)		
Alicyclic Hexanes *	*Water (v/v)*†	*Striped bass (v/w)*	*Bay shrimp (v/w)*
Cyclohexane	.54–10	N.D.‡– 48	4.4– 6.9
Methylcyclohexane	.54– 7.3	N.D.‡–130	16 – 26
Ethylcyclohexane	1.5 –11	5.8– 63	8.5– 66
1,1 Dimethylcyclohexane	1.5 – 8.7	23 –170	9.1–110
1,2 Dimethylcyclohexane	.32– 7.9	1.1–260	24 – 47
1,3 Dimethylcyclohexane	1.6 –12	6.5–160	7.0–100
1,4 Dimethylcyclohexane	1.2 – 7.1	28 – 46	12 – 36

* 1,2 and 1,4 dimethylcyclohexanes are mixtures of cis and trans isomers.
† v = Volume, w = Weight, Initial dosage
‡ N.D. = Non detectable below 0.7 μl/kg for tissue sample.

We noted that striped bass were more docile, easier to net and transfer after the 96 h testing period than before the dosing began. Striped bass exposed to the high dose of 1,3-DMCH (12 ppm) swam in tight clockwise circles instead of swimming around the aquaria like the control fish when the aquaria were disturbed. Some fish dosed with other alicyclics at lower concentrations would do the same but not as long (only 10–15 s).

DISCUSSION

The acute toxicity (24 h bioassay) of the alicyclics to striped bass and bay shrimp was in the low ppm range (1.5 to 10.9 μl/l) which is considered moderately toxic to fish and invertebrates relative to other compounds (Benville and Korn 1977). Extending the toxicity testing interval 3 more days resulted in increases in the toxicity of all bioassays except for two tests (striped bass/cyclohexane and bay shrimp/1,3 DMCH). The slight increase in toxicity was probably due to the delayed effects of the alicyclics since alicyclics rapidly escape from solution, resulting in alicyclic concentrations too low to cause acute effects. Using a continuous flow method of dosing would probably show higher toxicities (lower LC$_{50}$s). Static tests usually result in higher LC$_{50}$ values (lower toxicity) than continuous dosing because the concentration of the toxicant is decreasing and not being replenished using the static method.

Three of the alicyclics (ECH, 1,3 DMCH and 1,4 DMCH) had solubility values below their LC$_{50}$ concentration values for striped bass (Figure 3). Researchers usually use a solubilizing agent to disperse "insoluble" toxicants without knowing the effects of the solubilizers. Therefore, we did not use any dispersing agents in this study.

Striped bass appeared to be more sensitive to alicyclics than other fish species that have been tested. Pickering and Henderson (1966) reported 96 h TLms (median tolerance limits) of cyclohexane for fathead minnows, *Pimephales promelas*; bluegills, *Lepomis macrochirus*; goldfish, *Carassius auratus*; and guppies, *Lebistes reticulatus*, of 42, 45, 55 and 75 μl/l, respectively. These are 5 to 9 times higher than the toxic levels to striped bass. Jenkins, Klein and Cooper (1977) found an LC$_{50}$ of 84 μl/l for methylcyclohexane with golden shiners, *Notemigonus chrysoleucas*, 14 times the level of toxicity for striped bass. Although little data are available on the toxicity of higher homologs of cyclohexane to fish, mammals show an increase in the narcotic action and toxicity when alkyl groups are added to cyclohexane (von Oettingen 1942). We found that MCH, 1,1 DMCH, 1,2 DMCH and 1,4 DMCH were narcotic to striped bass. Perhaps ECH and 1,3 DMCH also would have been narcotic if their solubilities were higher.

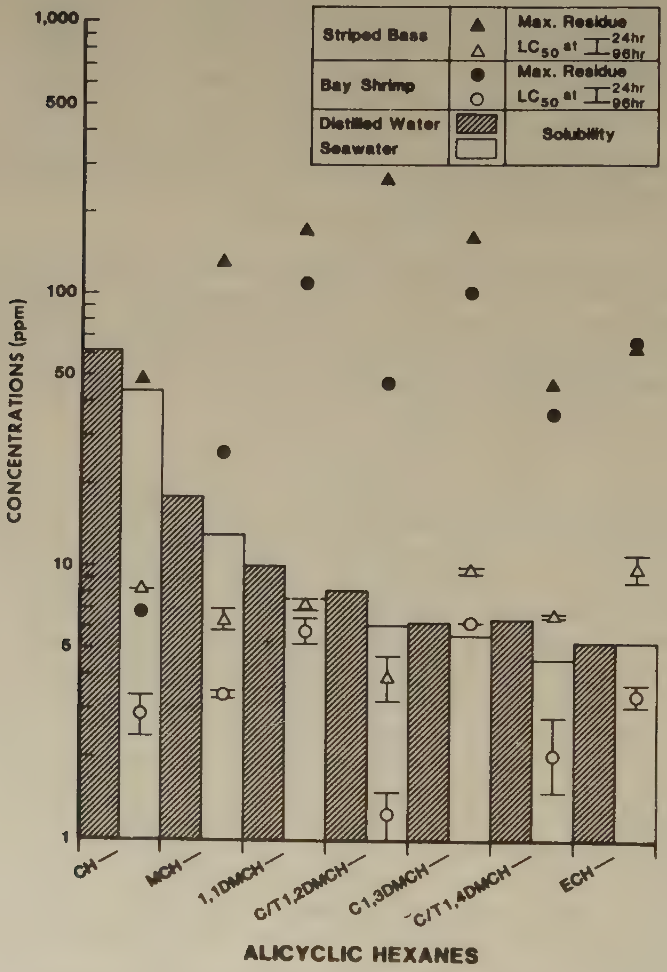

FIGURE 3. Solubilities, acute toxicities and maximum tissue residues of seven alicyclic hexanes.

Alicyclics bioaccumulated in striped bass and bay shrimp by factors of 33x and 13x, respectively. The greater accumulation in striped bass is due primarily to their higher lipid content. Alicyclic residues might have been much higher, as our research has indicated with monocyclic aromatic hydrocarbons (Whipple *et al.* 1981), if the samples were taken at the optimum exposure time. Aromatics accumulate rapidly in aquatic animals. Benzene (the simplest aromatic) accumulated in high concentrations in striped bass shortly after 40-min exposure (Whipple *et al.* 1981). A 1.5x to 119x increase above the ambient water concentration of benzene was noted depending on the tissue analyzed. Muscle had the lowest uptake and fat the highest uptake of the twelve analyzed tissues. Other scientists have shown that fish can accumulate monocyclic aromatic hydrocarbons from chemical mixtures, e.g. crude oil (Roubal, Stranahan and Malins 1978).

It has been suggested that cycloalkanes and other Water Soluble Fraction compounds from petroleum and its products may be more toxic than aromatics or that there is an additive effect with aromatics present (Caldwell, Caldarone and Mallon 1977). Further research should be conducted to study the interaction and combined effect of these two groups of cyclic compounds and to determine if the additive effects are manifested at the population and community levels.

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LITERATURE CITED

Benville, P. E., Jr., and R. C. Tindle. 1970. Dry ice homogenization procedure for fish samples in pesticide residue analysis. Agr. Food Chem., 18(5):948–949.

Benville, P. E., Jr., and S. Korn. 1977. The acute toxicity of six monocyclic aromatic crude oil components to striped bass *(Morone saxatilis) and bay shrimp (Crago franciscorum.)* Calif. Fish Game, 63(4):204–209.

Caldwell, R. S., E. M. Caldarone, and M. H. Mallon. 1977. Effects of Seawater-Soluble Fraction of Cook Inlet Crude Oil and Its Major Aromatic Components on Larval Stages of the Dungeness Crab, *Cancer Magister* Dana. Pages 210–220 *in* Douglas A. Wolfe, ed. Fate and Effects of Petroleum Hydrocarbons in Marine Ecosystems and Organisms, Pergamon Press, New York.

Connors, J. J., D. Jenkins and A. E. Greenberg (editors). 1981. Toxicity to fish. Pages 723–743 *in* Standard Methods for the Examination of Water and Wastewater. 15th edition, American Public Health Association, Washington, D.C.

Dean, J. A. (editor). 1979. Lange's Handbook of Chemistry. Physical Properties, Section 10:28–53. 12th edition, McGraw-Hill Book Co., NY.

Jenkins, D., S. A. Klein, and R. C. Cooper. 1977. Fish toxicity of jet fuels. *In* The toxicity of the synthetic fuel JP-9 and its components. Water Res., 11:1059–1067.

Korn, S. 1975. Semi-closed seawater system with automatic salinity, temperature and turbidity control. U.S. Dept. Commer., NOAA Tech. Rep. NMFS SSRF-694, 5p.

Litchfield, J. T., Jr., and F. Wilcoxon. 1949. A simplified method of evaluating dose-effect experiments. Pharmacol. Exper. Ther. J., 96:99–113.

Morrison, R. T., and R. N. Boyd. 1966. Organic chemistry, cyclic alipathic hydrocarbons. 2nd edition. Allyn and Bacon, Inc., Boston, MA. 1204 p.

Nunes, P., and P. E. Benville, Jr. 1979. Uptake and depuration of petroleum hydrocarbons in the Manila clam, *Tapes semidecussata* Reeve. Bull. Environ. Contam. Toxicol., 21:719–726.

Pickering, Q. H., and C. Henderson. 1966. Acute toxicity of some important petrochemicals to fish. Water Pollut. Control Fed. J. 38(9):1419–1429.

Roubal, W. T., S. I. Stranahan, and D. C. Malins. 1978. The accumulation of low molecular weight aromatic hydrocarbons of crude oil by coho salmon (*Oncorhynchus kisutch*) and starry flounder (*Platichthys stellatus*). Arch. Environ. Contam. Toxicol., 7:237–244.

von Oettingen, W. F. 1942. The toxicity and potential dangers of aliphatic and aromatic hydrocarbons. Yale J. Biol. Med., 15:167–184.

Whipple, J. A., M. B. Eldridge, and P. Benville, Jr. 1981. An ecological perspective of the effects of monocyclic aromatic hydrocarbons on fishes. Pages 483–551 *in* F. John Vernberg, Anthony Calabrese, Frederick P. Thurberg and Winona B. Vernberg, eds. Biological monitoring of marine pollutants. Academic Press, NY.

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Use of Pup Counts in Indexing Population Changes in Pinnipeds

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A series of population simulations were used to test the accuracy of estimating the discrete rates of population change (RPC) from annual pup counts. The simulations indicate that pup counts can give a biased estimate of RPC, and that the magnitude and direction of bias depends on which life history parameters are density dependent and on the maximum rate of population change. In general, if pre-census pup survival is density dependent the estimated RPC using pup counts is too low. If post-census pup survival is density dependent, the estimated RPC is too high. If adult survival is density dependent, there is very little bias in the estimate. The results indicate that pup counts can be reliable indicators of population growth, but caution should be used in interpreting the results unless density feedback mechanisms have been identified.

Les auteurs utilisent une série de simulations démographiques pour vérifier la précision des estimations des taux discrets de variation d'une population (TVP) effectuées à partir des recensements annuels de nouveaux-nés. Les simulations révèlent que ces dénombrements peuvent fournir une estimation biaisée du TVP et que les paramètres vitaux dépendant de la densité et le taux maximum de variation d'une population influent sur l'ampleur et la direction de la tendance. En général, le TVP calculé en fonction des recensements de nouveaux-nés est trop faible si la survie de ceux-ci avant le dénombrement dépend de la densité. Par contre, le TVP est trop élevé si la survie après le dénombrement dépend de la densité. L'estimation est très peu biaisée si la survie des adultes dépend de la densité. Les résultats révèlent que le recensement des nouveaux-nés constitue un indice fiable de la croissance démographique ; on doit toutefois interpréter les résultats avec prudence à moins d'avoir trouvé des mécanismes rétroactifs liés à la densité.

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For many species of pinnipeds, annual counts of pups provide the best available censusing method. These counts are used to estimate the rate of population change (RPC) by comparing percentage change in counts from year to year as in the case of California sea lions, *Zalophus californianus* (DeMaster et al. 1982); northern elephant seals, *Mirounga angustirostris* (Antonelis et al. 1981; Cooper and Stewart 1983); and Antarctic fur seal, *Callorhinus ursinus* (Chapman 1961; Eberhardt 1981; Fowler 1982). Recently, methods that rely on pup counts have also been developed to estimate whether the population is above or below the maximum net productivity level (MNPL), the point where the net growth rate of the population is maximized (DeMaster et al. 1982).

In this paper, an age structured simulation model is used to evaluate the accuracy of predicting population trends from a time series of pup censuses. We have assumed that the sex ratio of pups at birth does not change with population size, and therefore, models that utilize female pups only are suitable for predicting the direction and magnitude of bias in using pup counts to estimate the RPC. Possibly, biases in estimating RPC's with pup counts exist, and these biases may differ under different life history scenarios. If we can understand these biases and their causes, we can increase the predictive powers of the pup counts, or at least be aware of the limits when using pup counts to manage resources.

In the simulations we use life history parameters that are representative of most populations of pinnipeds (Eberhardt and Siniff 1977). The number of individuals in the first age class (1) is defined as the number of female pups at the time the census is made. In developing the model, three mechanisms of density dependence were investigated: density-dependent post-census pup survivorship, dependent on the number of pups in the population; density-dependent pre-census survivorship, dependent on the number of births in the population; and density-dependent adult survivorship, dependent on the number of non-pups in the population. Both types of pup survival are considered to be the most likely types of density dependence in the wild (Eberhardt 1977). Adult survival was selected because the population growth rate is most sensitive to its change (Goodman 1978, 1984). Fecundity and age at maturation were not investigated in depth because, as will be shown, they would provide the same sort of bias as does density dependence in pre-census pup survival. For simplicity, all types of density dependence were treated as linear functions.

Methods

Our age structure population models were written in the FORTRAN programming language. Initial parameters were selected to produce either an 8% or a 4% growth rate. These RPC's were considered reasonable for recovering populations of pinnipeds (Eberhardt and Siniff 1977). The model was

TABLE 1. Selected pinniped life history parameter values of given age classes (*denotes minimum values).

	Weddell seal[a]	Antarctic fur seal[b]	NW Atlantic harp seal[c]	Gray seal[d]
Annual survival rates of given age classes				
Birth–weaning		0.85		0.73
Weaning – age 1				0.90
Birth – age 1	0.76–0.82*	0.76–0.92	0.50–0.97	
Juvenile	0.48–0.50*	0.95		0.93
Adult	0.66–0.76*	0.92–0.95	0.90	0.94
Annual fecundity rates of given age classes				
Age 3	0.27	0.28		
Age 4	0.27	0.38		0.08
Age 5	0.27	0.42		0.28
Age 6 and older	0.40	0.45	0.46	0.42

[a] Stirling (1971).
[b] Payne (1977, 1979).
[c] Lett et al. (1981).
[d] Harwood (1981).

designed to handle a population with 25 year–age classes (Eberhardt and Siniff 1977). The probability of surviving through age class 25 was set at 0. A sample of life history parameter values reported for pinnipeds is listed in Table 1. The range of life history values used in the simulations is listed in Table 2.

The age classes followed a trajectory based on the following equations:

$$N_{1,t+1} = \sum_{x=1}^{25} N_{x,t} \cdot M_x$$

$$N_{x+1,t+1} = N_{x,t} \cdot P_x \qquad x = 1, 2, \ldots, 24$$

where P_x = the probability of survival from census at age x until census at age $x + 1$ and M_x = the probability of a female age x at year t having a female offspring at year $t + 1$.

For each case, the population level was initially set at 25% of the carrying capacity and allowed to continue to equilibrium. The RPC at time t was estimated by calculating

$$\text{RPC (total population)} = N_t / N_{t-1}$$

$$\text{RPC (pups)} = N\text{pups}_t / N\text{pups}_{t-1}.$$

The net population change was calculated as

$$\text{Delta (total population)} = N_t - N_{t-1}$$

$$\text{Delta (pups)} = N\text{pups}_t - N\text{pups}_{t-1}.$$

The bias of estimating the RPC by the pup growth rate was calculated as

$$\text{Bias} = \frac{\text{RPC (pups)} - \text{RPC (total population)}}{\text{RPC (total population)}}.$$

The three types of density dependence were tested with initial RPC's of 8 and 4% to see if changing the rate at which equilibrium is achieved changes the bias. Density-dependent post-census survival was calculated in the following way:

$$P(1, t) = P(1, k) + [P(1, i) - P(1, k)] \times \left[1 - \frac{N(1, t) - N(1, i)}{N(1, k) - N(1, i)}\right]$$

TABLE 2. Parameter values used in density dependence simulations.

	Model 1 (post-census pup survival)	Model 2 (pre-census pup survival)	Model 3 (adult survival)
Annual survival rates of given age classes			
Birth–census	1.00	0.40–1.00	1.00
Census – age 2	0.30–0.75	0.75	0.75
Age 2	0.85	0.85	0.85
Age 3	0.90	0.90	0.90
Age 4 – age 24	0.94	0.94	0.84–0.94
Annual fecundity rates of given age classes			
Age 4	0.10	0.04–0.10	0.09–0.10
Age 5	0.20	0.08–0.20	0.18–0.20
Age 6	0.30	0.12–0.30	0.27–0.30
Age 7 – age 24	0.40	0.16–0.40	0.36–0.40

where $P(1, t)$ = survival of age class 1 at time t, $N(1, t)$ = population of age class 1 at time t, k = time at which population is at carrying capacity, and i = time at which population is initially started.

Density-dependent pre-census survival was calculated in the following way:

$$G(t) = G(k) + [G(i) - G(k)] \cdot \left[1 - \frac{N(B, t) - N(B, i)}{N(B, k) - N(B, i)}\right]$$

where $G(t)$ = pre-census survival rate at time t and $N(B, t)$ = number of births at time t calulated by

$$N(B, t) = \sum_{x=1}^{25} F(x) \cdot N(x, t) \cdot P(x)$$

where $F(x)$ = fecundity for age class x conditional on female survival, $N(x, t)$ = population in age class x at time t, and $P(x)$ = survival of age class x.

Once $G(t)$ was calculated, it was used in the following equation to calculate the effective fecundity (Goodman 1984) for

TABLE 3. Results of density dependence simulations with three models. (RPC = rate of population change, MNPL = maximum net productivity level, EPL = equilibrium population level).

	Model 1 (post-census pup survival) initial growth rate		Model 2 (pre-census pup survival) initial growth rate		Model 3 (adult survival) initial growth rate	
	8%	4%	8%	4%	8%	4%
Percentage of EPL at true MNPL	68	58	67	58	52	52
Percentage of EPL at predicted MNPL	78	63	48	47	49	50
Percentage of EPL at predicted MNPL minus percentage of EPL at true MNPL	10	5	−19	−11	−3	−2
Bias in RPC at true MNPL	0.009	0.002	−0.018	−0.005	−0.002	−0.001
Largest bias in RPC	0.011	0.002	−0.027	−0.006	−0.002	−0.001
Time lag in years between true MNPL and predicted MNPL	−3	−3	+6	+7	+1	+1
Largest time lag in years	−4	−4	+15	+12	+3	+1

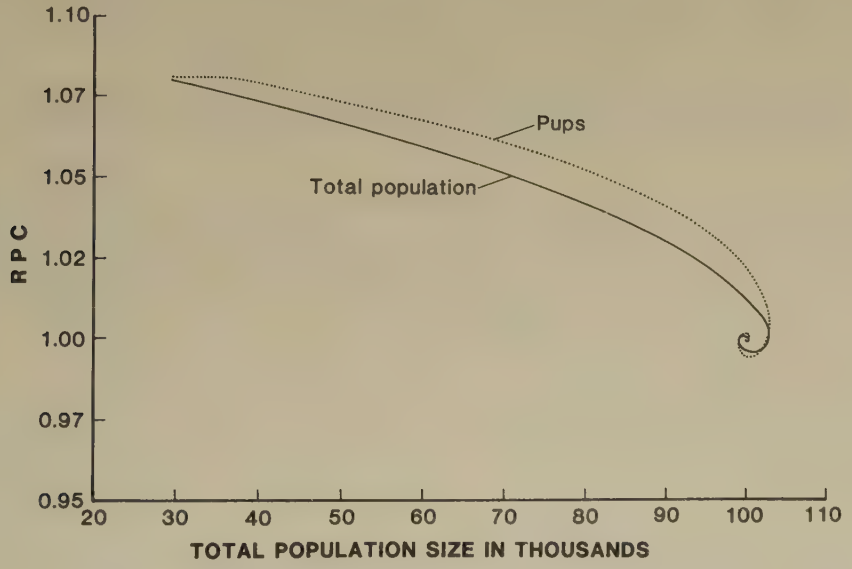

FIG. 1. Relationship of the RPC and the total population size when post-census pup survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

use in the Leslie matrix:

$$M(x, t) = F(x) \cdot P(x) \cdot G(t)$$

where $M(x, t)$ = effective fecundity of age class x at time t.

Density-dependent adult survival was calculated in the following way:

$$P(A, t) = P(A, k) + [P(A, i) - P(A, k)] \times \left[1 - \frac{N(NP, t) - N(NP, i)}{N(NP, k) - N(NP, i)}\right]$$

where $P(A, t)$ = survival of adult age classes at time t (adult age classes are 4 through 25) and $N(NP, t)$ = number of non-pups in the population at time t calculated by

$$N(NP, t) = \sum_{x=2}^{25} N(x, t).$$

The adult survival rate at time t was used to calculate $M(x, t)$ at each iteration of the simulation.

Results

Results of the six different simulations indicate that biases in estimating the RPC depends on the type of density dependence and the magnitude of the maximum RPC. Additionally, biases found in estimating the time when the MNPL is reached also depend on the type of density dependence and the magnitude of the RPC. Simulation results are discussed in three sections: density-dependent post-census pup survival (model 1), density-dependent pre-census pup survival (model 2), and density-dependent adult survival (model 3). A summary of results is provided in Table 3.

Density-Dependent Post-Census Pup Survival

When post-census pup survival is density dependent, the total population reacts more quickly than the pup population to the effects of the density dependence. Density-dependent post-census pup survival affects the number of individuals in the first

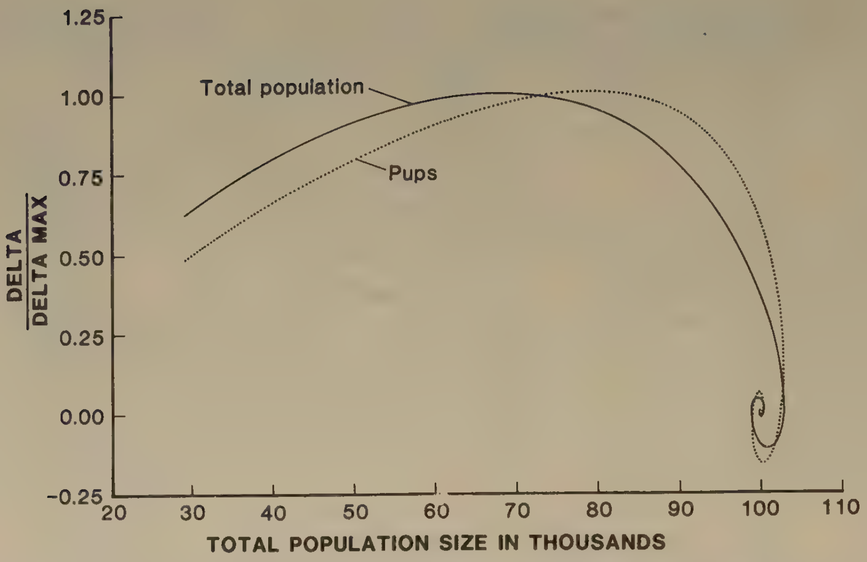

FIG. 2. Relationship of predicted and true production curves to total population size when post-census pup survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

age class that survive to the second age class. Therefore, any drop in survivability immediately acts on the number of individuals entering the second age class and, in doing so, acts on the total population as well. The first age class does not respond to the effects of the density dependence until the cohort that originally entered the second age class becomes capable of reproducing. Thus, the dynamics of the pup population lag behind the total population as the RPC declines (Fig. 1).

For the same reason, the production curve determined by pup counts lags behind the production curve of the total population (compared by measuring delta/delta max in both curves) (Fig. 2). In this case, delta max is the maximum change in the production curve.

In both the 8 and 4% growth simulations, the RPC of the pups lags behind the RPC of the total population. The time lag between the pups and the total population is the same in both simulations. However, the high initial RPC simulated population grows much larger during the time lag than the low initial RPC population. The difference between the true MNPL and the MNPL as indicated by the pup counts is larger for those simulations using higher initial rates of increase.

Density-Dependent Pre-Census Survival

In the case of density-dependent pre-census survival, the bias is in the opposite direction from that in the case of density-dependent post-census pup survival. Once again this bias can be explained to be a result of density dependence acting on a specific part of the age structure. Any decrease in pre-census survival immediately acts on the population in the first age class. The effect of this decreased survival is an immediate decline in the RPC of the number of pups. The RPC of the total population also declines but to a lesser degree, due to the buffering of the 24 unaffected age classes (Fig. 3). Once again the production curves also show this time lag (Fig. 4).

The 4% initial growth simulation again shows the same direction of bias as found in the 8% simulation. The magnitude of the bias in terms of time lags in the two production curves is similar, although in the 4% simulation it is slightly less than in the 8% simulation. This translates into a smaller population difference between the two peaks of the production curves, due again to the lower population increase in the same amount of time as seen in the simulation with 4% initial growth.

Density-Dependent Adult Survival

In the case of density-dependent adult survival, the decreasing survival rate affects both the adult age classes (5–25) and the pup age class (1). Therefore, a much smaller bias is created. This is because adult survival affects the number of pups entering the first age class the following year. Any given decrease in adult survival affects all age classes other than the juveniles (ages 2, 3, and 4) in the next time step. Having three age classes with unchanging survival rates in turn causes the total population's RPC to decline slightly behind the pup population's RPC (Fig. 5). The magnitude of this bias is much smaller than is seen in the previous two types of density dependence. Once again, the production curves follow this same pattern (Fig. 6).

Discussion

The simulations we described indicate that the type of density dependence affecting a population can bias estimates of RPC based on pup counts. For example, estimates of replacement yield and MNPL that rely on pup counts are probably biased. The direction of bias, however, can be inferred if the density-dependent mechanisms are known.

Managers should be aware of these biases and should incorporate them in the development of management policy. The following comparisons of density dependence found in the wild and its effects on estimating population changes using simultations will, hopefully, illustrate this point.

To infer a direction of bias in the use of pup counts to estimate

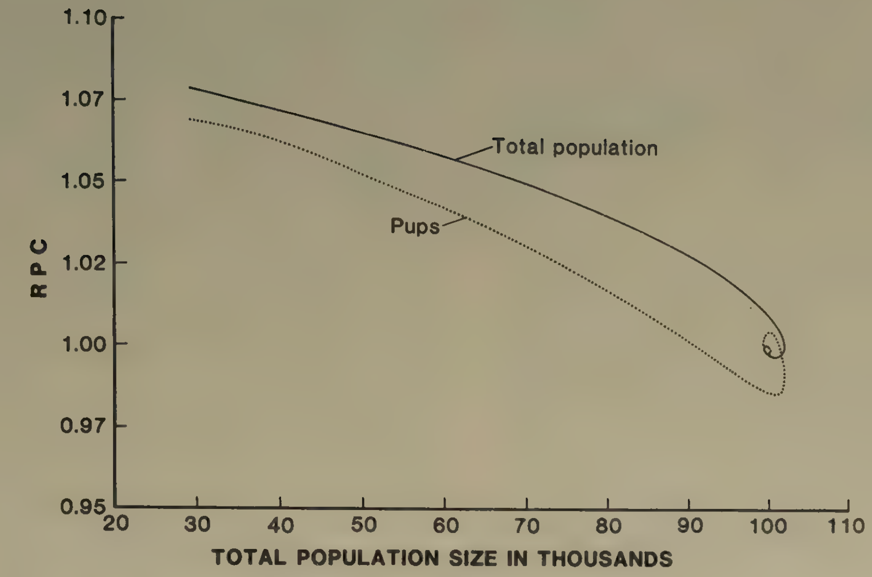

FIG. 3. Relationship of the RPC and the total population size when pre-census pup survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

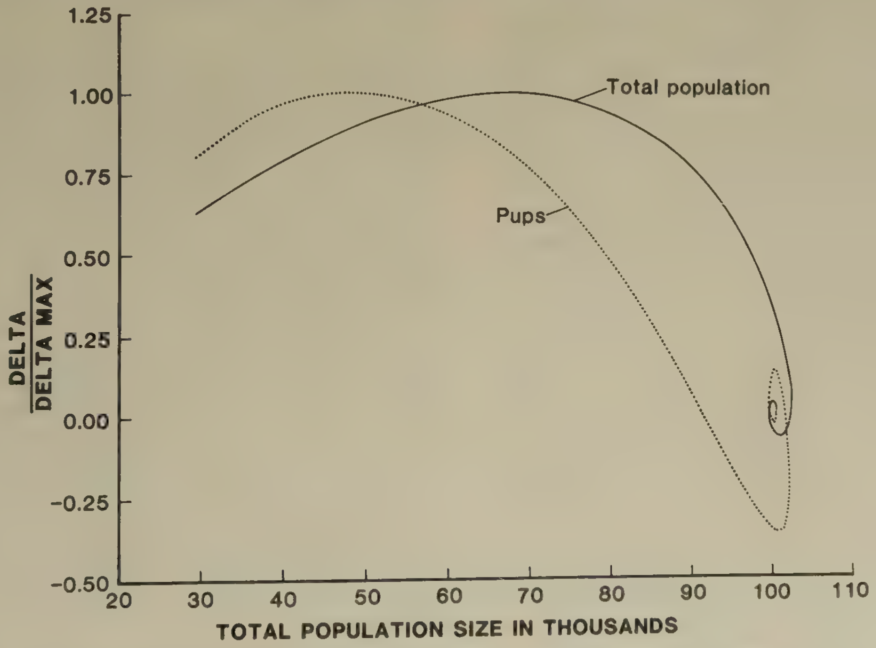

FIG. 4. Relationship of predicted and true production curves to total population size when pre-census pup survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

the RPC, it is reasonable to look at the available data on what parameters are density dependent in pinnipeds. Eberhardt (1977) suggested that pup survival (both pre- and post-census) is more likely to be density dependent than either adult fecundity or adult survival. Adult fecundity would cause the same direction of bias as pre-census pup survival, since both act on the first age class. However, because pre-census pup survival is more likely to be density dependent than adult fecundity (Eberhardt 1977), it was chosen for modeling.

Density-dependent pup production has been described in many pinniped species (for summary see Fowler et al. 1980). For gray seal, *Halichoerus grypus*, this mechanism has been described to act on pups between the age of birth and weaning (Coulson and Hickling 1964; Bonner 1975; Harwood 1981).

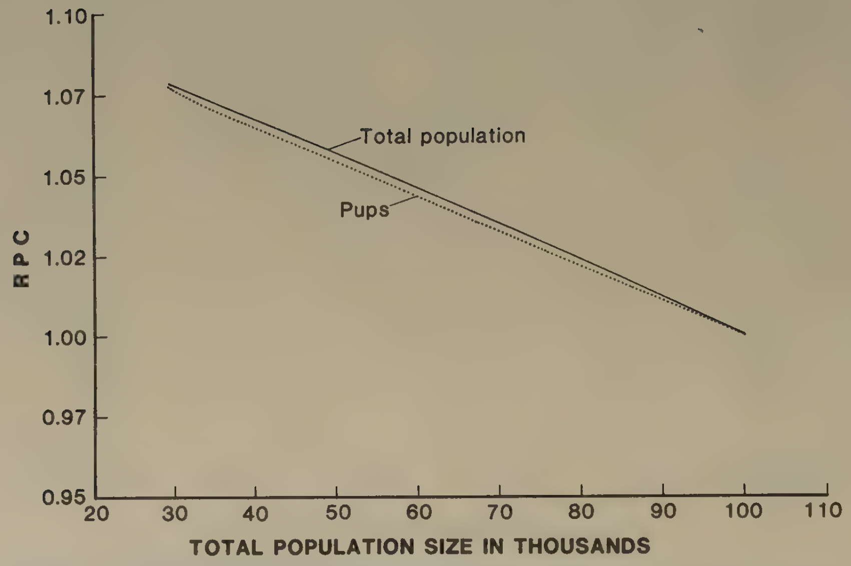

FIG. 5. Relationship of the RPC and the total population size when adult survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

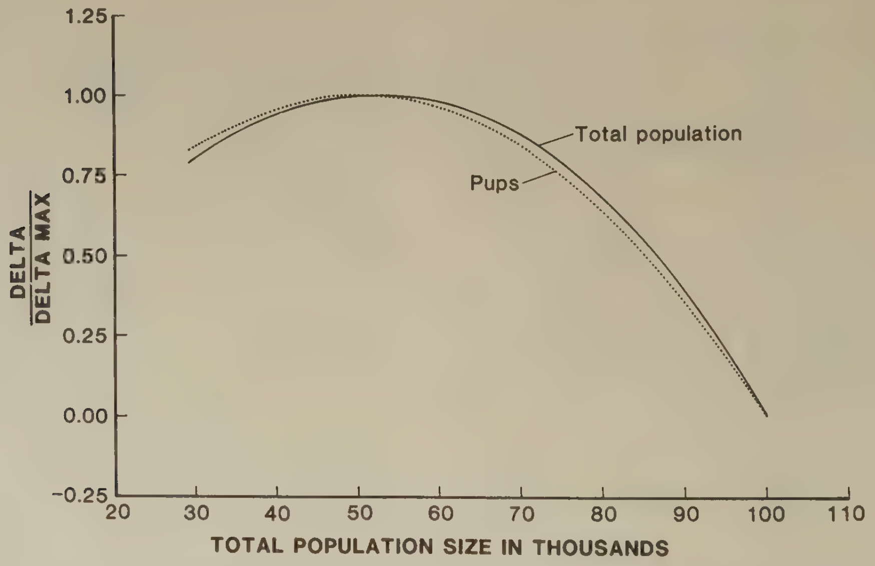

FIG. 6. Relationship of predicted and true production curves to total population size when adult survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

Density-dependent birth rates have been described in northwestern Atlantic harp seals, *Phoca groenlandica* (Lett and Benjaminsen 1977; Lett et al. 1981). Northern fur seals were the first of many pinniped species to have shown evidence of density-dependent age at maturation (Scheffer 1955). In all three types of density dependence described, the density dependence is assumed to act on the first age class and would cause the pup population to lead the total population both in the decline of the RPC and in passing the peak on the production curve as shown in the pre-census pup survival model.

The results of the two simulations where pre-census survival is density dependent indicate that pup counts provide a conservative estimate of the RPC. This absolute value of bias can be as high as 3% in the case of an initial growth rate of 8%. In addition, using pup counts to determine whether a population is above or below the MNPL is not conservative. That is, pup counts (under this type of density dependence) indicate that a population is above the MNPL before the population actually reaches the MNPL.

Density-dependent juvenile survival has been reported in pinnipeds, as in the northwestern Atlantic harp seal (Lett and Benjaminsen 1977; Lett et al. 1981). In this case, density dependence acts on the juvenile age classes rather than on the first age class. This would cause the pup counts to trail the total population both in the decline in the RPC and in passing the peak on the production curve as demonstrated above in the post-census simulation.

In both simulations where post-census pup survivorship is density dependent, pup counts lag behind the total population, or in other words, pup counts overestimate the true RPC of the population and are late in estimating the time at which peak productivity occurs. The largest bias in the RPC is one percentage point; it occurs in the vicinity of the MNPL. The bias in estimating peak production is −3 yr. This means that if post-census survival is density dependent, pup counts are conservative in indicating whether or not a population is above or below its MNPL.

Evidence of density-dependent adult survival in pinnipeds is difficult to obtain, if it does exist, due to the complications in obtaining accurate data. For those species where it is demonstrated to occur, pup counts would be accurate in predicting the population RPC and the relative position on the production curve as was seen in the adult survival model.

Possibly more than one type of density dependence may be operative (Smith and Polacheck 1981). Given the mechanisms we have proposed in this paper (i.e. pre-census pup survival and post-census pup survival) the resultant bias would be a combination of the two independent biases and would self-cancel to some extent.

Possibly, nonlinear density dependence is a more reasonable mechanism than linear density dependence (Fowler 1981). The difference in bias between models with linear and nonlinear density dependence would clearly be in magnitude rather than direction. The difference in resulting bias is unknown at this time. Future work will address these issues.

In order to use the predictions of this paper, managers need to know the type of density-dependent mechanisms acting on the population. If the density dependence acts on the pups, either through adult fecundity, age at maturation, or pup survival prior to census, the bias would cause the pup population to lead the total population both in the decline of the RPC and in passing the peak on the production curve. If the density dependence acts on the pups after census, the pup population would trail the total population both in the decline of the RPC and in passing the peak on the production curve.

We conclude with a particular example of how the results of our study can be used to determine the status of a stock from pup counts. It has been suggested that the San Miguel Island population of California sea lions is above the MNPL (DeMaster et al. 1982). Based on data from the years 1975 to 1981 on San Miguel Island (DeMaster et al. 1982), a regression of the survival rate of pre-census pups versus number of pups born did not show a slope significantly different from zero. In addition, most of the sea lions that are "salvaged" by rehabilitation centers each spring are yearlings in an emaciated condition. This was particularly evident in the spring of 1983, when winter storms were unusually severe. If we can assume that post-census survival is density dependent and that pre-census survival is not affected by density, then we can increase our confidence in this status assessment based on the conclusions of our model. In this case, the population should be even closer to the equilibrium population level than is indicated by the pup counts.

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References

ANTONELIS, G. A., JR., S. LEATHERWOOD, AND D. K. ODELL. 1981. Population growth and censuses of the northern elephant seal, *Mirounga angustirostris*, on the California Channel Islands, 1958–1978. Fish. Bull. U.S. 79(3): 562–567.

BONNER, W. N. 1975. Population increase of grey seals at the Farne Islands. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 169: 366–370.

CHAPMAN, D. B. 1961. Population dynamics of the Alaska fur seal herd. Trans. N. Am. Wildl. Nat. Resour. Conf. 26: 356–369.

COOPER, C. F., AND B. S. STEWART. 1983. Demography of northern elephant seals, 1911–1982. Science (Wash., DC) 219: 969–971.

COULSON, J. C., AND G. HICKLING. 1964. The breeding biology of the grey seal, *Halichoerus grypus* (Fab.) on the Farne Islands, Northumberland. J. Anim. Ecol. 33: 485–512.

DEMASTER, D. P., D. J. MILLER, D. GOODMAN, R. L. DELONG, AND B. S. STEWART. 1982. Assessment of California sea lion fishery interactions. Trans. N. Am. Wildl. Nat. Resour. Conf. 47: 253–264.

EBERHARDT, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environ. Conserv. 4(3): 205–212.

1981. Population dynamics of the Pribilof fur seals, p. 197–220. *In* C. W. Fowler and T. D. Smith [ed.] Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. J. Fish. Res. Board Can. 34: 183–190.

FOWLER, C. W. 1981. Density dependence as related to life history strategy. Ecology 62(3): 602–610.

1982. Interactions of northern fur seals and commercial fisheries. Trans. N. Am. Wildl. Nat. Resour. Conf. 47: 278–292.

FOWLER, C. W., W. T. BUNDERSON, M. B. CHERRY, R. J. RYEL, AND B. B. STEELE. 1980. Comparative population dynamics of large mammals: a search for management criteria. Report Number MMC-77-20 to the United States Marine Mammal Commission. National Technical Information Service NTIS PB80-178627, Springfield, VA.

GOODMAN, D. 1978. Management implications of the mathematical demography of marine mammals. NTIS (PB-289 678): 65 p.

1984. Statistics of reproductive rate estimates and their implications for population projection. Rep. Int. Whaling Comm. Spec. Issue 6: 161–173 (ISBN 0906975 07 7).

HARWOOD, J. 1981. Managing gray seal populations for optimum stability, p. 159–172. *In* C. W. Fowler and T. D. Smith [ed.] Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

LETT, P. F., AND T. BENJAMINSEN. 1977. A stochastic model for the management of the northwestern Atlantic harp seal (*Pagophilus groenlandicus*) population. J. Fish. Res. Board Can. 34: 1155–1187.

LETT, P. F., R. K. MOHN, AND D. I. GRAY. 1981. Density-dependent processes and management strategy for the Northwest Atlantic harp seal population, p. 135–157. *In* C. W. Fowler and T. D. Smith [ed.] Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

PAYNE, M. R. 1977. Growth of a fur seal population. Phil. Trans. R. Soc. Lond. B 279: 67–79.

1979. Growth in the Antarctic fur seal *Arctocephalus gazella*. J. Zool. (Lond.) 187: 1–20.

SCHEFFER, V. B. 1955. Body size with relation to population density in mammals. J. Mammal. 36(4): 493–515.

SMITH, T. D., AND T. POLACHECK. 1981. Reexamination of the life table for northern fur seals with implications about population regulatory mechanisms, p. 99–120. *In* C. W. Fowler and T. D. Smith [ed.] Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

STIRLING, I. 1971. Population dynamics of the Weddell seal (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica, 1966–1968, p. 141–161. *In* W. H. Burt [ed.] Antarctic Pinnipedia. American Geophysical Union, Washington, DC.

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STOMACH CONTENTS OF ALBACORE, SKIPJACK, AND BONITO CAUGHT OFF SOUTHERN CALIFORNIA DURING SUMMER 1983

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ABSTRACT

Three species of scombrids were troll-caught off southern California for a food habits study during Cruise 166 of NOAA research vessel *David Starr Jordan* in August 1983, to examine effects of the anomalous oceanography (El Niño) of that period. The stomachs of 94 albacore (*Thunnus alalunga*), 31 skipjack (*Katsuwonus pelamis*), and 42 bonito (*Sarda chiliensis*) were examined. Chi-square analysis for homogeneity showed highly significant differences in types of prey and proportions consumed by the three species. Albacore consumed 96.8% fish, 35.1% cephalopods, and 52.1% crustaceans by frequency of occurrence, and 82.4% fish, 1.7% cephalopods, and 15.9% crustaceans by numerical frequency. Skipjack consumed 19.4% fish, 12.9% cephalopods, and 54.8% crustaceans (45.2% euphausiids) by frequency of occurrence, and 11.1% fish, 2.6% cephalopods, and 86.3% crustaceans (76.5% euphausiids) by numerical frequency. Bonito consumed 71.4% fish and 26.2% crustaceans (11.9% euphausiids) by frequency of occurrence, and 32.1% fish and 67.9% crustaceans (63.4% euphausiids) by numerical frequency. A comparison to historical data during similar and dissimilar environmental conditions suggests that the scombrids are opportunistic predators, and that prey availability was partly a function of the oceanographic conditions. The index of relative importance and mean volumetric ratio measurement of northern anchovy (*Engraulis mordax*) in the diet of albacore is presented.

RESUMEN

Con el fin de examinar los efectos oceanográficos anómalos (El Niño) en el período de agosto de 1983, durante la campaña 166 del buque de investigación de la NOAA "David Starr Jordan" para un estudio de hábitos alimentarios, se capturaron con línea tres especies de escómbridos a la altura del sur de California. Se examinaron 94 contenidos estomacales de albacora (*Thunnus alalunga*), 31 de listado (*Katsuwonus pelamis*), y 42 de bonito (*Sarda chilensis*). Análisis de chi-cuadrado para homogeneidad demostraron diferencias altamente significativas en los tipos y proporciones de presas consumidas por las 3 especies. Por frecuencia de registro, la albacora consumió un 96.8% de peces, 35.2% de cefalópodos, y 52.1% de crustáceos; mientras que por frecuencia numérica los valores fueron, peces: 82.4%, cefalópodos: 1.7%, y crustáceos: 15.9%. El listado consumió 19.4% de peces, 12.9% de cefalópodos, y 54.8% de crustáceos (45.2% de eufáusidos) por frecuencia de registro; en frecuencia numérica los valores fueron, peces: 11.1%, cefalópodos: 2.6%, y crustáceos: 86.3% (76.5% de eufáusidos). El bonito consumió 71.4% de peces, y 26.2% de crustáceos (11.9% de eufáusidos) por frecuencia de registro, y 32.2% de peces y 67.9% de crustáceos (63.4% de eufáusidos) por frecuencia numérica.

La comparación con datos históricos similares durante condiciones ambientales semejantes y diferentes sugiere que los escómbridos son predadores oportunísticos, y que la disponibilidad de presas era, parcialmente, el resultado de las condiciones oceanográficas. Se presentan el índice de importancia relativa y medidas de la tasa volumétrica media de la anchoveta del norte (*Engraulis mordax*) en la dieta de la albacora.

INTRODUCTION

The limitations of single-species models in fisheries management have been recognized and well documented (Anderson and Ursin 1977; Laevastu and Larkins 1981; and Livingston MS[1]). That predation mortality can control year-class strength of a given prey species has been established and deserves further examination (Laevastu and Larkins 1981; Rothschild and Forney 1979). We conducted a multispecies comparison by examining stomach contents of three species of scombrids—skipjack (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), and Pacific bonito (*Sarda chiliensis*)—collected in the California Current during the 1983 El Niño. Food habits studies from El Niño and other periods are also reviewed here.

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[1] Livingston, P.A. MS. Marine fishery management demands on fish food habits data: a discussion of alternative uses of food habits data for management purposes. NMFS, Resource Ecology and Fishery Management Division, 7600 Sand Point Way, N.E., Bldg. 4, Bin c15700, Seattle, Washington, 98115, 16 p.

We found significant amounts of young-of-the-year anchovies, *Engraulis mordax*, in the diet of these scombrids, especially albacore. A number of animals prey on the northern anchovy, including at least 33 species of fish, seabirds, marine mammals, and man (Radovich 1979). The impact of predation and adverse environmental conditions on a commercially important fish like the northern anchovy could have far-reaching economic repercussions.

Prior to Iversen's (1962) study on albacore in the central and northeast Pacific Ocean, food habits studies on albacore were largely nonquantitative (Clemens and Iselin 1963; McHugh 1952; Powell and Hildebrand 1949; Hart 1942; and Hart and Hollister 1947). In the 1970s, more quantitative studies were undertaken, including those by Pinkas et al. (1971) and Iversen (1962). Both studies were conducted when El Niño events were mild or absent.

Most food habits studies on skipjack have taken place in the central and eastern tropical Pacific Ocean (Alverson 1963; Nakamura 1965; and Waldron and King 1963). However, Alverson's study in the eastern tropical Pacific Ocean includes the region between Point Conception and 20°N, between 123° to 115°W during another strong El Niño (1957-59).

There is a paucity of literature on bonito's food habits in the California Current. One other study, spanning two years of collection (1968 and 1969—mild El Niño years), was available for comparison (Pinkas et al. 1971).

METHODS

The three scombrid species (94 albacore, 41 Pacific bonito, and 21 skipjack) were caught by hand-operated jig lines with artificial lures trolled at an average speed of 6 knots, during Cruise 166 of NOAA research vessel *David Starr Jordan*. In addition, 1 bonito and 10 skipjack were caught in gill nets deployed at night. Size of fish caught was fairly homogeneous within each species (Table 1). The albacore and bonito were caught in water approximately the same temperature (17.8°C and 17.3°C); the skipjack were caught in the warmer water (21.2°C) of the Southern California Bight (Table 1).

The albacore and bonito were caught in close association with each other, within 100 miles of shore, between 33°59′ to 36°44′N and 121°19′ to 122°30′W. The skipjack were all taken south of Point Conception in the Southern California Bight between 32°38′ to 33°46′N and 117°57′ to 119°16′W (Figure 1).

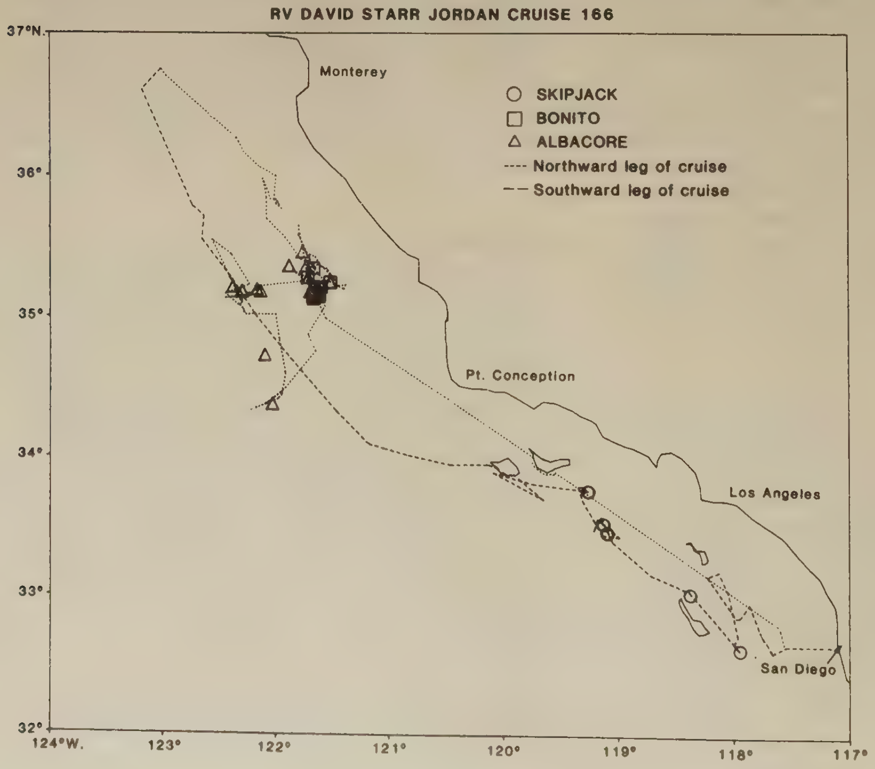

Figure 1. Capture locations of albacore, skipjack, and bonito during Cruise 166 of R/V *David Starr Jordan*, August 15-September 1, 1983.

TABLE 1

Mean Fork Lengths and Standard Deviations, and Mean Water Temperatures at Time of Catch

		Albacore ($n=94$)	Skipjack ($n=31$)	Bonito ($n=42$)
FL. (cm)	$\bar{x}$	69.3	48.7	59.9
	(s)	(8.817)	(2.031)	(1.902)
Temp. (°C)	$\bar{x}$	17.77	21.17	17.32
	(s)	(0.624)	(0.442)	(0.252)

Stomachs were removed aboard the ship and frozen. Contents were thawed in the laboratory and rough-sorted. Because many prey items in the stomachs in this study have not yet been identified, they were pooled into gross taxonomic categories, usually at the class level, except where otherwise indicated. In order to compare our data with previous studies, we pooled (whenever possible) the data from those studies to correspond to our fewer categories.

Percent frequency of occurrence (number of stomachs in which a particular prey occurred as a percentage of the total number of stomachs = %FO) and percent numerical frequency (%NF) were determined for all three species. Additionally, anchovies were separated from the other fish found in the albacore stomachs. The percent volumes of anchovies and other fish prey were determined.

We calculated a measure of relative importance (Pinkas et al. 1971) for the fish consumed by 85 albacore. This value, termed index of relative importance (IRI), is the product of the sum of the numerical plus volumetric percentages of a given prey item and percent frequency of occurrence of that prey [IRI = %FO(%NF + %VF)]. It is used here for comparison of anchovies consumed relative to all other fish prey combined and not as a total IRI for all prey items.

The data from the 85 albacore stomachs that contained fish were also examined individually to determine the importance of a given prey to an individual predator. Individual stomach analysis is similar in principle to an IRI calculation; however, instead of pooling prey from all of the stomachs of a given predator, one evaluates the distribution of fractional volumes and numbers of prey for each stomach. In contrast to the IRI, these data make it possible to determine the variance, mean, and standard deviation, and to perform statistical tests. The mean volumetric or numerical ratio measurement (MVRM, MNRM) was based on the percentages or proportions of prey in relation to total stomach volume or total numbers of all prey in individual stomachs (Ankenbrandt, in press). We calculated the MVRM for anchovies in the diet of albacore by the following equation (and MNRM can be calculated similarly):

$$\bar{r}_j = \frac{\sum_{i=1}^{N} r_{ij}}{N} = \text{mean volumetric ratio of prey } j \text{ to the total volume of } N \text{ stomachs}$$

where N = number of stomachs examined

$$r_{ij} = \frac{V_{ij}}{\left[\sum_{j=1}^{n} V_{ij}\right]} = \text{ratio of prey } j \text{ to the total volume of stomach } i$$

and where V_{ij} = volume of prey type j in stomach i

n = number of prey items

In an attempt to determine if the albacore were consuming anchovies at random, we performed a runs test (Sokal and Rohlf 1969) to test the null hypothesis that the frequency of occurrence of anchovies within the albacore stomachs is random.

It appeared that the three predator species were not eating the same kinds of prey items in the same proportions. We used Crow's (1982) suggestion for showing differences in feeding habits by analysis of stomach contents using a 2-way, R x C, contingency table, where R is the number of prey categories and C is the predator species.

RESULTS

Scombrid Feeding Habits

Chi-square analysis for homogeneity showed highly significant differences in types of prey and proportions consumed by the three scombrid species (Table 2).

TABLE 2

Observed Frequency

Prey	Predator			
	Skipjack	Albacore	Bonito	Total
Unident. Crust.	6	71	13	90
Pleuroncodes	4	84	0	88
Amphipods	8	20	19	47
Hyperiidae	1	18	0	19
Euphausiids	148	916	449	1513
Fish	22	5741	228	5991
Cephalopods	5	117	0	122
Total	194	6967	709	7870

Minimum estimated expected value is 0.47
Independence of prey occurrence was tested, and the null hypothesis of homogeneity was rejected. Chi-square value = 1,641.721, probability <0.0001.

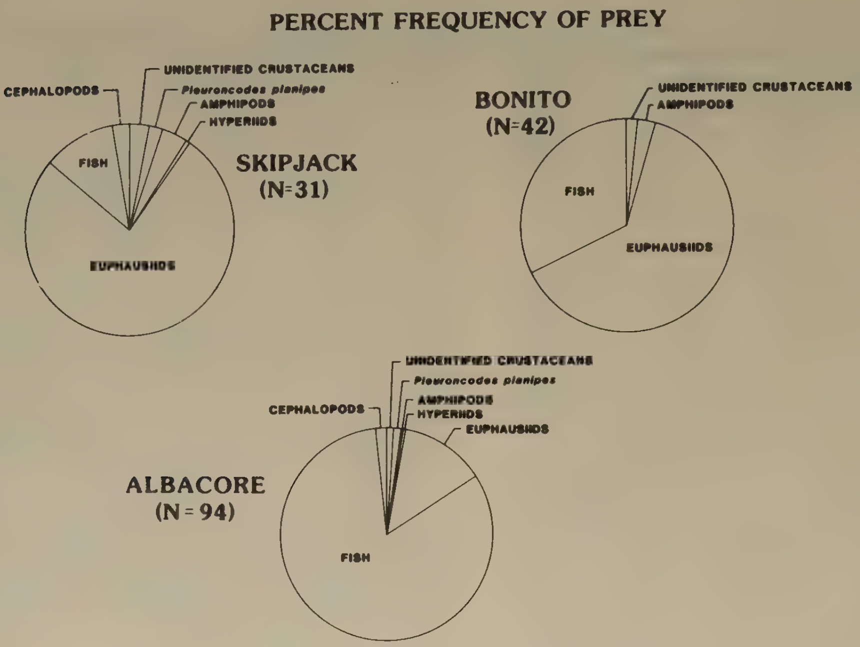

Figure 2. Percent numerical frequency of prey consumed by three scombrids (skipjack, albacore, and bonito) caught during Cruise 166.

Skipjack consumed crustacea most frequently (FO = 54.8%) and in greatest numerical frequency (NF = 86.3%). Bonito consumed fish most frequently (FO = 71.4%), but crustacea were highest in numerical frequency (NF = 67.0%) (Figures 2 and 3). The crustacean most important to both skipjack and bonito was the euphausiid *Nyctiphanes simplex*.

The primary prey of albacore was fish (FO = 96.8%, NF = 82.4%) (Figures 2 and 3). The IRI for anchovies in the diet of albacore was 7,630; for al

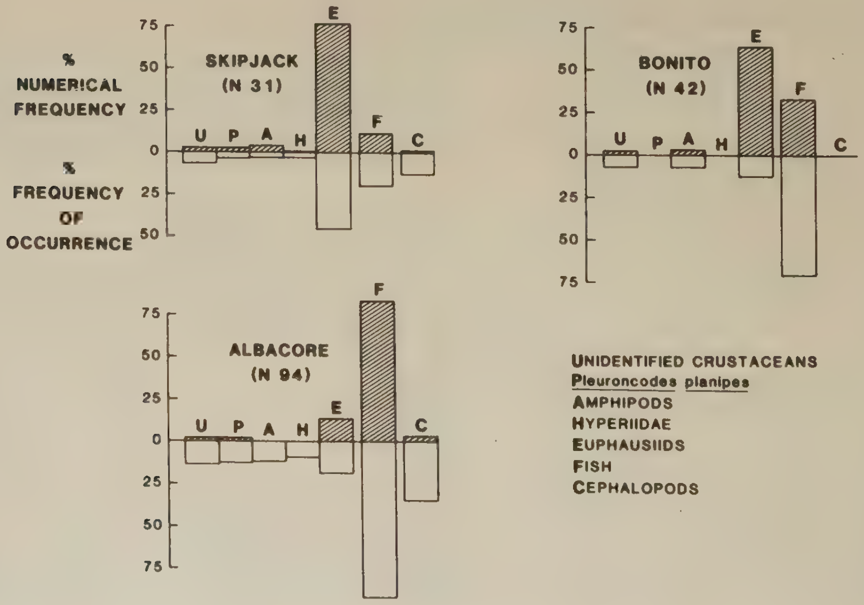

Figure 3. Percent numerical frequency and percent frequency of occurrence of prey consumed by skipjack, albacore, and bonito caught during Cruise 166.

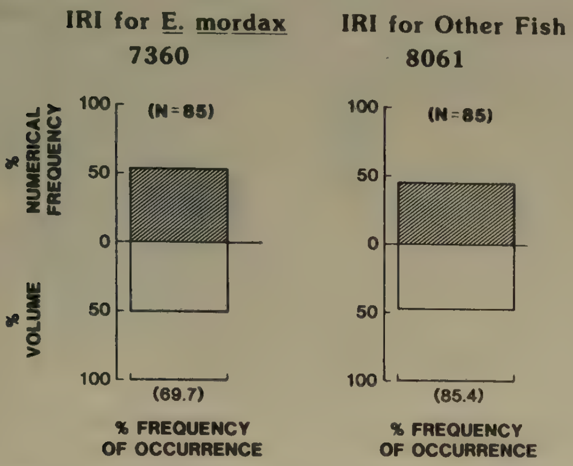

Figure 4. Index of relative importance and percent numerical frequency, percent volumetric frequency, percent frequency of occurrence for anchovies and other fish consumed by albacore caught during Cruise 166.

other fish combined, the IRI was 8,061 (Figure 4). The anchovies found in the albacore stomachs were young-of-the-year, from 22-47 mm SL, with a mean of 33.6 mm and a standard deviation of 4.97 (Figure 5). Albacore stomachs can be a source for verifying the existence or abundance of the anchovy size classes that are underrepresented in the California reduction fishery sampling program used for anchovy population studies (Mais 1981).

The presence of *Pleuroncodes planipes*, pelagic red crab, in the diets of skipjack and albacore is notable because the crab's northern limit in most years appears to be 28°N, in Sebastian Viscaino Bay (Longhurst 1967).

Individual Stomach Analysis

The mean volumetric ratio measurement for anchovies in albacore stomachs (0.092) was only a little less than the mean volumetric ratio measurement for all other fish combined (0.11) (Table 3).

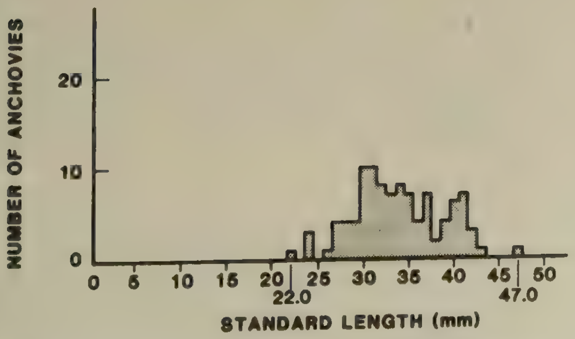

Figure 5. Length-frequency distribution of anchovies found in albacore stomachs caught during Cruise 166.

TABLE 3

Mean Volumetric Ratio Measurements (MVRM) and Standard Deviations of Anchovies and All Other Fish Consumed by 85 Albacore

	E. mordax	Other fishes
MVRM	0.092	0.110
(s)	0.144	0.207

The mean numerical percentage of anchovies in albacore stomachs is somewhat less ($\bar{x}$ = 42.4%) than all other fish combined ($\bar{x}$ = 57.6%), as was the mean volumetric percentage of anchovies ($\bar{x}$ = 44.1%) to all other fish combined ($\bar{x}$ = 55.9%) (Table 4).

The mean volumetric and numerical percentages of anchovies from individual stomach analyses were also less than the numerical and volumetric percentages of anchovies in the IRI calculation (Table 5).

Cumulative frequency plots showing the proportions of percent numerical and volumetric frequencies of anchovies in albacore stomachs (Figures 6 and 7) demonstrate that there were more albacore stomachs containing fish other than anchovies than stomachs containing anchovies alone.

The runs test resulted in rejection of the null hypothesis of random distribution of anchovies in albacore stomachs at the 5% significance level. Ancho-

TABLE 4

Mean Volumetric and Numerical Percentages and Standard Deviations of Anchovies and Other Fish Consumed by 85 Albacore

	E. mordax	Other fishes
Numerical percentage		
$\bar{x}$	42.4%	57.6%
(s)	39.7	39.7
Percent volume		
$\bar{x}$	44.1%	55.9%
(s)	41.2	41.2

TABLE 5

Percentages Used in IRI Calculation

	E. mordax	Other fishes
Numerical percentage	53.9%	46.1%
Percent volume	51.7%	48.3%
Frequency of occurrence	69.7%	85.4%

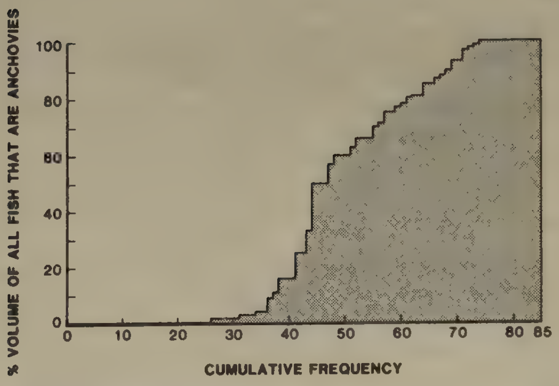

Figure 6. Cumulative frequency plot of volumetric percentage of all anchovies in 85 albacore stomachs.

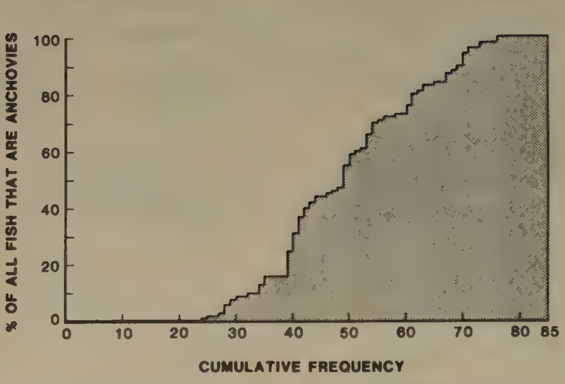

Figure 7. Cumulative frequency plot of numerical percentage of all anchovies in 85 albacore stomachs.

vies were present in some of the albacore stomachs in large quantities; and some stomachs did not contain any anchovies. This finding is not necessarily a reflection of active selection, but more likely an indication of the patchy distribution of the anchovy schools.

DISCUSSION

There are significant differences in types of prey and proportions consumed among the three scombrids. Bonito and skipjack consumed more euphausiids than any other type of prey. Albacore consumed more fish than any other prey, and the northern anchovy, *Engraulis mordax*, was consumed nearly as much as all other fish combined.

The 1983 El Niño event resulted in, among other things, a marked decrease in the southward transport of the California Current. The decreased transport correlates with a decrease in zooplankton biomass (Chelton et al. 1982) and a decrease in the occurrence of cephalopods off the California coast. In addition, fauna endemic to more southerly ranges (e.g., *Pleuroncodes planipes* and *Nyctiphanes simplex*) were transported northward and incorporated into the diets of the scombrid predators. A comparison of this study with other food habits studies during El Niño periods showed similar trends.

Pacific Bonito

In 1968 and 1969 (Pinkas et al. 1971), fish were the primary prey for bonito, with cephalopods next in importance (in 1968, NF for cephalopods = 13.9% and FO = 21.3%; in 1969, NF = 5.8% and FO = 28.2%). However, in our study, the importance of crustacea is about the same as fish (Figure 8). No

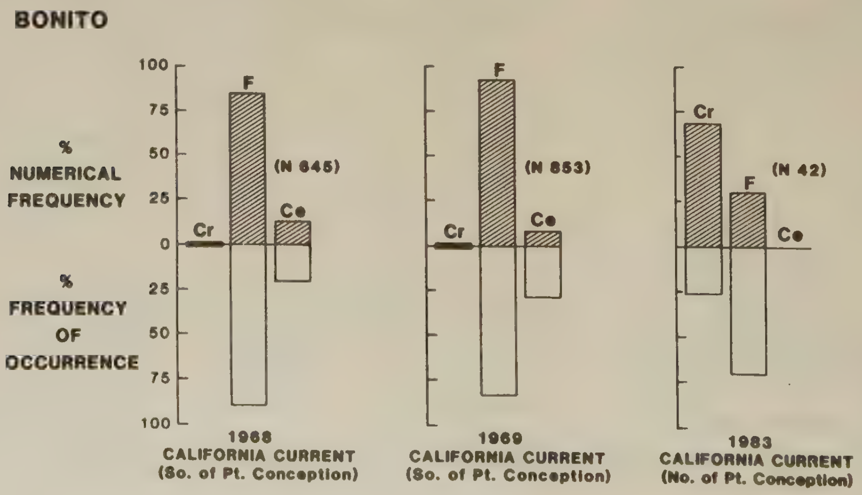

Figure 8. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by bonito caught in 1968 and 1969 (Pinkas et al. 1971) and those caught from August 15-September 1, 1983. Cr = crustaceans, Ce = cephalopods, and F = fish.

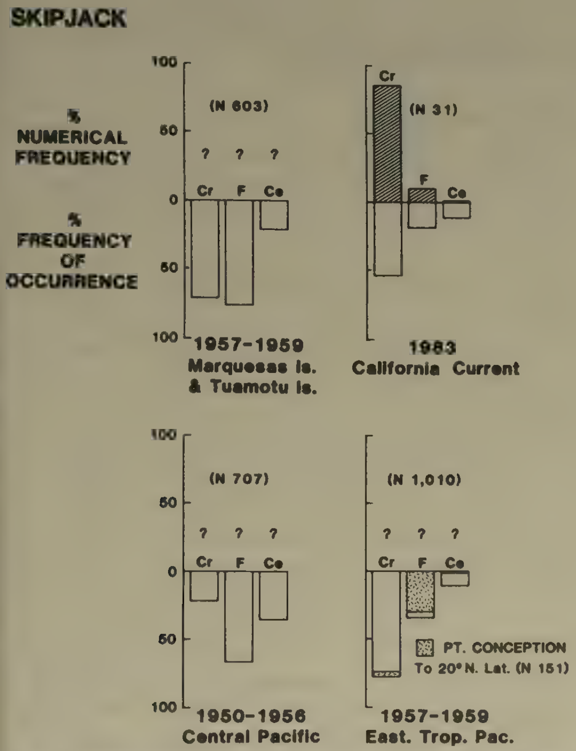

Figure 9. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by skipjack in several studies. On left are studies from central and south Pacific: 1957-59 (Nakamura 1965), and 1950-56 (Waldron and King 1963). On right are studies from the eastern tropical Pacific and California Current: 1983 (this study) and 1957-59 (Alverson 1963). Question marks represent unavailable data. Cr = crustaceans, Ce = cephalopods, and F = fish.

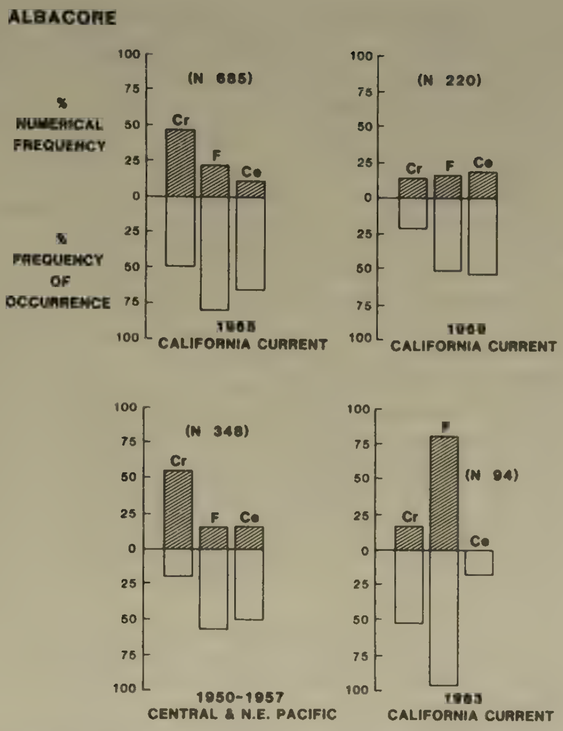

Figure 10. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by albacore in 1968 and 1969 (Pinkas et al. 1971), 1950-57 (Iversen 1962), and 1983 (this study). Cr = crustaceans, Ce = cephalopods, and F = fish.

cephalopods were found in the bonito stomachs collected during the 1983 cruise. This suggests that cephalopods were not available to the bonito we sampled during the 1983 El Niño.

Skipjack

In Alverson's (1963) study conducted in the region between Point Conception and 20°N during the 1957-59 El Niño, crustacea were consumed most frequently, as in 1983 (Figure 9). In contrast to 1983, when euphausiids were the most important crustacean, the pelagic red crab was the most important crustacean in 1957-59.

Albacore

We used Pinkas et al. (1971) for a detailed comparison to our study because of the similar location (Iversen's 1962 data from the equatorial and northeastern Pacific were pooled together). Fish were the primary prey in 1968 and 1969, with anchovies the most important species in 1968, and sauries (*Cololabis saira*) the most important species in 1969 (Figure 10). In 1983, anchovies were almost equal in importance to all other fish combined.

MVRM versus IRI

The MVRM and the numeric and volumetric proportions (used in IRI calculations) gave similar results: anchovies were consumed almost as much in volume and numbers as all other fish combined. The mean numerical and volumetric percentages of anchovies consumed by albacore were slightly less (42.4% and 44.1%, respectively) than the numerical and volumetric percentages used for the IRI calculation (53.9% and 51.7%). This reflects the difference between establishing a measurement based on a pooled average (volumetric and numerical proportions) and a weighted average (MVRM and MNRM). The fact that numerical and volumetric proportions based on pooled (IRI-type) data are greater than the means of volumetric and numerical frequency shows that some albacore were primarily consuming anchovies, whereas, at other times, other albacore were consuming more of some other fish species. This suggests that the complementary use of the MVRM and volumetric frequency and the MNRM and the numerical frequency will provide insight into the feeding habits of fishes.

The MVRM calculation enabled us to perform statistical tests on these data and resulted in the conclusion that the distribution of anchovies as prey among individual albacore was not random. That is, it appears that some albacore encountered and fed on anchovy schools, while other albacore encountered and fed on schools of other fish, a possible reflection of the inherently patchy distribution of anchovy schools.

Gill-Raker Gap and Prey Size

In a previous study (Magnuson and Heitz 1971), the gill-raker gap (space between the first two gill rakers of the first gill arch) was measured or estimated by linear regression in tunas, mackerels, and dolphinfish. The results showed a positive correlation between gill-raker gap and fork length, and gill-raker gap and prey size—i.e., the predators with smaller gill-raker gaps consumed smaller prey.

We determined the mean gill-raker gaps for the scombrids in our study by linear regression (fork length vs gill-raker gap). Although bonito had a larger gill-raker gap (ca. 3.05 mm) than both skipjack (ca. 1.03 mm) and albacore (ca. 2.50 mm), we found that the proportion of prey items in bonito stomachs more closely resembled the contents of skipjack stomachs (mostly euphausiids) than albacore stomach contents.

Our findings were contrary to those of Magnuson and Heitz: most of the bonito prey were smaller than most of the albacore prey, even though albacore had a smaller gill-raker gap than bonito and they were caught in the same area on the same days. This information, added to the evidence that scombrids in previous studies have diverse and opportunistic feeding habits during similar and dissimilar environmental conditions, underscores the complexities of food-web dynamics.

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LITERATURE CITED

Alverson, F.G. 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. IATTC Comm. Bull. VII (5):295-459.

Andersen, K.P., and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. Meddr Danm. Fisk-og Havunders, N.S. 7:319-435.

Ankenbrandt, L.G. In press. Food habits of bait-caught skipjack tuna (*Katsuwonus pelamis*) from the southwestern Atlantic ocean. Fish. Bull., U.S.

Chelton, D.B., P.A. Bernal, and J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40(4):1095-1125.

Clemens, H.B., and R.A. Iselin. 1963. Food of Pacific albacore in the California fishery (1955-1961). FAO Fish. Rep. Exp. paper (30) 3(6):1523-1535.

Crow, M.E. 1982. Some statistical techniques for analyzing the stomach contents of fish. *In* G.M. Cailliet and C.A. Simenstad (eds.), GUTSHOP '81 Fish Food Habits Studies Proc. Third Pac. Workshop. Wash. Sea Grant Pub., Univ. Wash, Seattle.

Hart, J.L. 1942. Albacore food. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. (52):9-10.

Hart, J.L., and H.J. Hollister. 1947. Notes on the albacore fishery. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. (71):3-4.

Iversen, R.T.B. 1962. Food of albacore tuna, *Thunnus germo* (Lacepede), in the central and northeastern Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 62(214):459-481.

Laevastu, T., and H.A. Larkins. 1981. Marine fisheries ecosystem: its quantitative evaluation and management. Fishing News Books, Ltd. Farnaham, Surrey, England, 162 p.

Longhurst, A.R. 1967. The biology of mass occurrences of Galatheid crustaceans and their utilization as a fisheries resource. Proc. World Scientific Conf. on the Biol. and Culture of Shrimps and Prawns. FAO Fish Rep. 2(57):95-110.

Magnuson, J.J., and J.G. Heitz. 1971. Gill raker apparatus and food selectivity among mackerels, tunas and dolphins. Fish. Bull., U.S. 69(2):361-370.

Mais, K.F. 1981. Age-composition changes in the anchovy, *Engraulis mordax*, central population. CalCOFI Rep. 22:82-87.

McHugh, J.L. 1952. The food of albacore (*Germo alulunga*) off California and Baja California. Scripps Inst. Oceanogr., Bull. 6(4):161-172.

Nakamura, E.L. 1965. Food and feeding habits of skipjack tuna (*Katsuwonus pelamis*) from the Marquesas and Tuamotu Islands. Trans. Am. Fish. Soc. 94(3):236-242.

Pinkas, L., M.S. Oliphant, and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dept. Fish Game, Fish Bull. 152, 84 p.

Powell, D.E., and H.A. Hildebrand. 1949. Albacore tuna exploration in Alaskan and adjacent waters—1949. U.S. Fish Wildl. Serv., Fish. Leaflet 376, 33 p.

Radovich, J. 1979. Managing pelagic schooling prey species. *In* R.H. Stroud (compiler) and H. Clepper (ed.), Predator-prey systems in fisheries management. Sport Fishing Inst., Wash. D.C., p. 365-375.

Rothschild, B.J., and J.L. Forney. 1979. The symposium summarized. *In* R.H. Stroud (compiler) and H. Clepper (ed.), Predator-prey systems in fisheries management. Sport Fishing Inst., Wash. D.C., p. 487-496.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco, 776 p.

Waldron, K.D., and J.E. King. 1963. Food of skipjack in the central Pacific. FAO Fish. Rep. Exp. Paper (26),6(3):1431-1457.

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USING OBJECTIVE CRITERIA AND MULTIPLE REGRESSION MODELS FOR AGE DETERMINATION IN FISHES

George W. Boehlert[1]

ABSTRACT

Analysis of the age structure of exploited fish populations is necessary for models upon which management decisions are made, but existing aging methodology for many species is hindered by subjective criteria used in age determination. A new technique is described in which age is estimated using multiple regression models based upon the measurable parameters otolith weight, otolith length, and otolith width in the splitnose rockfish, *Sebastes diploproa*, and the canary rockfish, *S. pinniger*. Models were calibrated using ages determined by interpretation of both whole otoliths and otolith sections which differ within these species, particularly at greater lengths. The models typically explained from 70 to 92% of the variability in age depending upon species, sex, and method of age analysis. In another sample used to verify the precision of the models, variability associated with model-estimated ages was generally less than that induced by variability in ages between different agencies. Based upon the pattern of otolith growth in length, width, and weight in these and other species, it is suggested that these methods would be applicable to a wide variety of fishes. Implementation of this type of age determination methodology could result in savings in time and cost for fisheries management agencies while decreasing variability among age estimates between different laboratories.

Virtually all methods of age determination in fishes involve a certain degree of subjectivity. Deciding whether a mark on an otolith or scale constitutes 1 year's growth is difficult; precision in fish aging improves only with experience. Even so, variability between experienced readers may be great. Sandeman (1969), for example, observed only 9% agreement between readers for a wide age range of otoliths of *Sebastes marinus* and *S. mentella*, and noted greater variability with increasing age of the fish. Kimura et al. (1979) suggested that bias between readers within a given agency is likely to be much less than among different agencies. In a situation such as exists on the Pacific coast, where several management agencies may routinely determine ages for the same species, interagency calibrations are necessary but are rarely achieved. Williams and Bedford (1974) suggested "...that otolith reading remains, for the present at least, as much an art as a science, and that proficiency cannot easily be achieved without examination of very large numbers of otoliths." Clearly, objective, repeatable age determination methodology which will minimize variability is desirable.

Traditional methodology for age determination in fishes generally involves some calcified structure; in *Sebastes*, Six and Horton (1977) tested 25 different structures. By far the most commonly used structures, however, are the otolith and scales. Scales are often best for short-lived, fast-growing species because annuli become indistinct near the margin in long-lived, slower growing species (Power 1978; Maraldo and MacCrimmon 1979). When this is the case, the otolith becomes the superior structure for age determination; even in the otolith, however, annuli may become indistinct on the margin as otoliths thicken and become opaque with age. For this reason several investigators have used broken or sectioned otoliths to determine age from internal banding patterns. While some studies using otolith sections have provided clear continuation of growth patterns obvious on whole otoliths from younger specimens, others have suggested maximum ages which are double or triple those estimated from whole otoliths. Power (1978), for example, suggested ages of >50 yr in *Salvelinus namaycush* and *Coregonus clupeaformis* and provided confirming evidence based upon population structure. In the redfish, *Sebastes marinus*, Sandeman (1961) suggested that specimens exceeding 50 yr of age were present in the population; ages up to 80 yr have since been estimated (Sandeman[2]). Similarly, Beamish

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(1979b) estimated ages approaching 90 yr in certain Pacific species of *Sebastes*, including *S. alutus*. In the genus *Sebastes*, these estimates of extended longevity have recently been confirmed by Bennett et al. (1982), who used geochronological methods to confirm age in *S. diploproa*. Understanding population structure for such long-lived species will require a large number of age estimates using otolith sections. Routine sectioning and interpretation of otoliths, however, is a time-consuming process, and age structure would need to be determined frequently for management of an active fishery. In this paper I suggest a possible alternative method for age determination.

Otolith growth begins with the initial "focus" and thereafter by incremental concretions of calcium carbonate in the form of aragonite. Otolith size increases with increasing size and age of the fish. Differential addition of crystalline material to the otolith, however, results in a species-specific shape (Bingel 1981). In flatfish and certain other species, Williams and Bedford (1974) observed continued linear growth of the otolith with growth of the fish only until maximum size was achieved; beyond this time, the otolith began to thicken. This has been observed in several other species (Blacker 1974a). Linear measurements of the otolith (i.e., length and width) are directly related to fish length and show little variability, but otolith thickness and weight are highly variable in larger fish (Templeman and Squire 1956; Beamish 1979a, b).

Templeman and Squire (1956) observed that length and width of otoliths from slow- and fast-growing populations of haddock did not differ at the same fish length, whereas otolith weight was consistently greater in the slower growing (and therefore older) populations at a given length. The same trend appears to exist in some members of the genus *Sebates* (G. W. Boehlert unpubl. data).

Beamish (1979a) observed an increase in thickness of the hake otolith with increasing otolith section age and a nearly linear relationship of otolith thickness and otolith weight. If otolith thickness, and therefore weight, is a function of fish age, then if fish length (or otolith length, since the two are related) is known, one should be able to estimate fish age. This was suggested by Brander (1974) with Irish Sea cod. The objective of this study is to determine the trends of otolith growth in terms of thickness, length, width, and weight, and to determine the potential of these criteria for estimation of age in splitnose rockfish, *S. diploproa*, and canary rockfish, *S. pinniger*.

MATERIALS AND METHODS

Otolith Collection

Otoliths of *S. pinniger* and *S. diploproa* were collected during the 1980 West Coast Survey conducted by the Northwest and Alaska Fisheries Center on the FV *Pat San Marie* and the FV *Mary Lou*. Gear and sampling strategy were similar to that described in Gunderson and Sample (1980). Otoliths were collected from fish captured in all hauls until desired numbers of specimens in specified length categories were obtained. Both otoliths from each specimen were removed, cleaned, and stored in individual, labeled vials containing 50% ethanol. Data taken with each specimen included vessel, haul (with latitude, longitude, and bottom depth), sex, and fork length (to the nearest 0.1 cm). After returning to the laboratory, otoliths were thoroughly cleaned and the preservative renewed.

Age Determination

General information on otolith morphology and whole otolith aging methodology in *Sebastes* is described in detail by Kimura et al. (1979). Age determined from whole otoliths followed the aging methodology of Boehlert (1980) for *S. diploproa* and that of Six and Horton (1977) for *S. pinniger*. Ages determined in this manner are referred to as whole otolith ages.

Otolith sections were prepared for selected specimens using the left otolith after the methodology of Nichy[3] with several modifications. Specimens were affixed to heavy-duty cardboard tags with double-faced tape and embedded in polyester casting resin in preparation for sectioning. Specimens were mounted in a chuck specifically designed to accommodate the cardboard tags and fed onto a pair of thin diamond blades separated by acetate spacers on a Buehler[4] low-speed Isomet saw. Dorsal-ventral sections through the focus and perpendicular to the sulcus, about 0.4 mm thick, were removed from the center of the otolith. Sections were removed from the tag and attached to labeled microscope slides with histological mounting medium. They were subsequently ground to eliminate surface artifacts, first with 400-grit carborundum paper and then polished with 3 μm jeweler's rouge.

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

To compare internal otolith section annuli with surface annuli, 25 whole left otoliths from *S. pinniger* and 50 from *S. diploproa* were selected. Sample size was chosen to represent the range of ages estimated from whole otoliths. I determined the distance from focus to each annulus on the whole otolith along the dorsal-ventral axis from focus to dorsal edge of the otolith using an ocular micrometer on a dissecting microscope. These measurements were used to identify the first several annuli on corresponding sections. By following these identified annuli around to the internal dorsal surface it was determined that each small ring in the direction of counting (from focus to dorsal, interior surface) corresponded to a single year of growth (Fig. 1).

Sections were initially examined under a dissecting microscope at 30× magnification with either reflected light and a black background or transmitted light, depending upon the clarity of the annuli. Discerning and counting the narrow zones in otoliths from older fish was facilitated by the use of a compound microscope interfaced with a video camera and television screen. A more accurate estimate of age was made possible by the increased magnification and enhanced contrast of the compound microscope, coupled with the ease of viewing annuli on an enlarged screen.

Sections were aged by identifying the first translucent annulus (winter growth zone) and counting sequential growth zones from the center to the dorsal edge. Subsequent annuli were followed from the dorsal edge to the interior dorsal quadrant (after Beamish 1979b), and counted to the internal surface. In this paper, ages determined by different methods and sources will be discussed; none of these ages is known with certainty. For this reason, given ages will be defined as "standard ages" only for purposes of comparison.

Calibration Subsample

To establish models of age based upon otolith dimension and weight criteria, otoliths from the entire collection were subsampled. Every fourth otolith pair of *S. diploproa* and every third of *S. pinniger* were selected to provide roughly equal sample sizes representative of all sizes and collection (latitudinal) areas. These subsampled otoliths were used to develop the multiple regression models (see section on Data Analysis) and were treated as described below.

Whole otolith ages were determined by an experienced otolith reader to whom fish length remained unknown. This practice has been recommended by Williams and Bedford (1974), among others, to minimize bias in otolith reading. Otoliths were then dried to a constant weight at 58°C and placed in a dessicator for 8 h. Intact left otoliths were weighed to the nearest milligram. Otoliths were measured with dial calipers in the anteroposterior dimension (length) to the nearest 0.02 mm and in the maximum dorsoventral di-

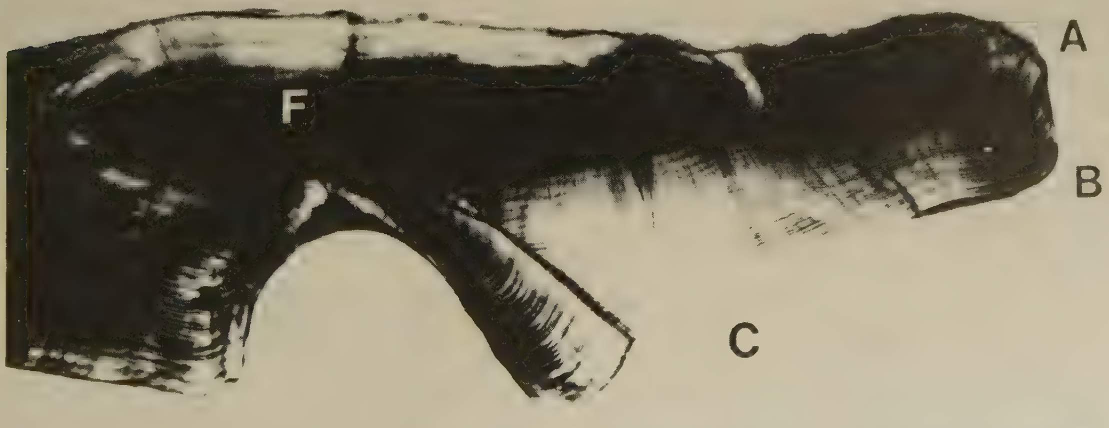

FIGURE 1.—Dorsal-ventral section of the left otolith of a 305 mm FL female *Sebastes diploproa*. Whole otolith ages are generally determined from the focus (F) to the dorsal edge (A), but often extend to the posterior margin (not shown) which may include additional annuli extending to greater ages (A to B). Section ages are determined from the focus (F) to the internal dorsal surface (C). Note the additional growth zones on axis F-C which have been deposited after the latest visible zones on axis F-A. The otolith section age of this specimen is 40 yr.

mension (width) to the nearest 0.05 mm. When the left otolith was chipped or broken, the right one was substituted for measurements, since no systematic differences between left and right otolith measurements were apparent for either species. The left otolith was subsequently sectioned and age determined by the same otolith reader. Otolith thickness, which is too variable to measure on the whole otolith, was measured on the section from internal to external surface just dorsal to the sulcus (Fig. 1).

Confirmation Subsample

In order to test the precision of the model, subsamples of 50 otoliths by sex and species were drawn randomly from samples not used in the calibration subsample. These samples were handled in the following way: A second whole otolith age was determined by reader A to determine within-reader variability for *S. diploproa* and between-reader variability for *S. pinniger* (reader B had left this laboratory). The otoliths were sent to the Northwest and Alaska Fisheries Center (Seattle, Wash.) for an additional whole otolith age to determine between-agency variability. The otolith was dried, weighed, measured, and sectioned as described above; a single otolith section age for each specimen was determined by reader A for both species. Model-estimated ages were determined by use of the multiple regression models described below.

Data Analysis

Generally, data were recorded in a standard format and stored on the Oregon State University Cyber 70 computer. Data management and analysis were assisted by use of the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975).

From the calibration subsample of otoliths, predictive regression equations were developed to estimate age from otolith morphometrics. Multiple regression models were fitted in the following form:

$$\text{Age} = b_1X_1 + b_2X_2 + b_3X_3 + b_nX_n + c$$

where age (years) is determined by conventional methods, b_n's = regression coefficients, X_n's = independent variables, and c = constant. Models were developed for males and females separately within each species with both otolith section ages and whole otolith ages as dependent variables. Independent variables included otolith weight, otolith length, otolith width, the respective square and cubic terms of each, and the interaction variables (otolith weight/otolith length and otolith length/otolith width). With the exception of otolith weight, where both weight and the cube of weight were used as independent variables, square or cubic terms were not used if the raw values were entered. This decreased problems of multicollinearity. Models were fitted in a forward stepwise manner (Nie et al. 1975) with the inclusion level for independent variables set at $P = 0.10$.

The 1980 confirmation subsample was used to verify the models. Direct comparisons between ages determined for the same otoliths but different reading methods were accomplished by paired *t*-tests. Since age is not known with certainty for any otolith, the ages determined by reader A for *S. diploproa* and by reader B for *S. pinniger*, which were used to calibrate the models in the calibration subsample, were considered as "standard age". To conduct multiple comparisons of variability, deviations from standard age were defined as follows: "model-induced variation" is the difference between the standard age and the model-predicted age; "within-agency variation" is the difference between ages determined by reader A for *S. diploproa* and between readers A and B for *S. pinniger*; "between-agency variation" is the difference between the standard age and the age determined by the National Marine Fisheries Service (NMFS). A one-way analysis of variance (ANOVA) was used to compare these deviations. Multiple range testing was conducted using the least significance difference method with $\alpha = 0.05$. This analysis was conducted only for whole otoliths since only a single section age was determined on the 1980 confirmation subsample.

RESULTS

Sebastes diploproa

Locations of the collections of *S. diploproa* are shown in Figure 2; this species was taken from lat. 36°49′ to 48°47′N and over a depth range of 62 to 338 m. The distribution was similar to that noted in 1977 (Boehlert 1980). A total of 975 male and 1,145 female specimens were taken during the survey. The length frequencies show a mode near 23 cm for males and 24 cm for females with secondary modes at 26 and 27 cm, respectively. Corresponding age frequencies (based upon whole otoliths) show a clear mode at 7 yr for both males and females, with whole otolith age ranges from 1 to 46 for males and 0 to 55 for females. Mean lengths-at-age for males and females are similar until age 8, after which females grow more rapidly (Boehlert 1980; Boehlert and Kappenman 1980).

Subsampling every fourth pair of otoliths from all collections of *S. diploproa* resulted in 290 female and 246 male specimens. The subsample was representative of the latitudinal distribution, age range, and length range of the whole collection. Capture, otolith, and age data from these samples are summarized in Table 1. Otolith section ages, as expected, were typically greater than whole otolith ages (Table 1); this was particularly true at greater lengths. Correlation matrices of pertinent otolith and age data (Table 2) show that otolith weight has the strongest linear association with otolith section age; both otolith weight and age are exponential functions of fish length. Plotting otolith length, fish length, and otolith weight against otolith section age demonstrates the pattern of otolith growth (Fig. 3). Past an age of about 25 yr, both otolith length and fork length reach approximate asymptotes, whereas otolith weight continues to increase. The wide fluctuations in otolith weight apparent at older ages correlate closely with changes in fork length (Fig. 3); for this reason, otolith weight alone is a relatively poor predictor of fish age at greater ages where fork length is highly variable. Addition of otolith

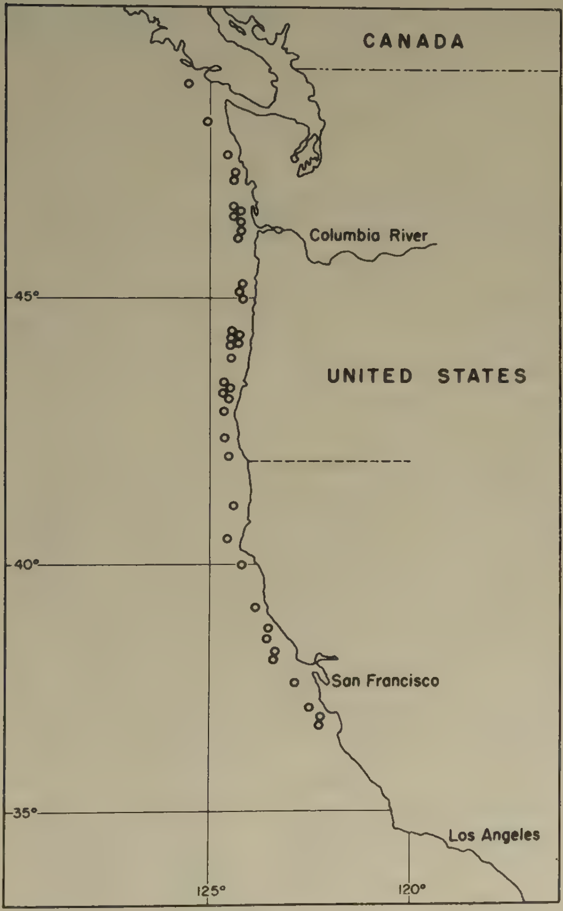

FIGURE 2.—Locations of 1980 West Coast Survey collections from which otoliths of *Sebastes diploproa* were taken.

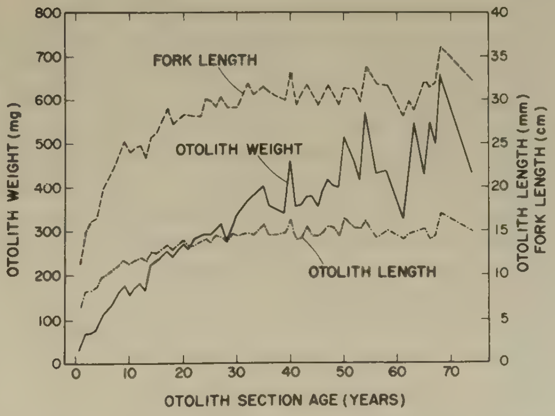

FIGURE 3.—Otolith characteristics of male *Sebastes diploproa* from the calibration subsample as related to fish length and age. N = 246. Note the covariation among the three curves, particularly at older ages.

TABLE 1.—Summary of biological and otolith data from the subsampled groups of *Sebastes diploproa* used in developing the age models.

	Females (N = 290)				Males (N = 246)			
Variable	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Depth of capture (fathoms)	34	185	137	29.36	53	185	136	28.45
Fork length (mm)	130	378	264	56.16	94	364	246	48.19
Otolith length (mm)	7.71	18.02	12.49	2.35	5.47	17.03	11.82	2.14
Otolith width (mm)	5.08	11.25	7.97	1.31	3.59	10.32	7.57	1.14
Otolith thickness (mm)	0.83	2.97	1.41	0.44	0.73	2.84	1.35	0.39
Otolith dry weight (mg)	59	724	244.6	150.4	25	659	208	117.4
Whole otolith age (yr)	1	56	15.2	11.97	1	40	13.5	9.78
Otolith section age (yr)	2	66	17.2	15.68	1	74	16.9	16.41

TABLE 2.—Correlation matrix for selected otolith morphometric, weight, and age data for the calibration subsample of *Sebastes diploproa*.

	Otolith weight	Otolith length	Otolith width	Otolith thickness	Whole otolith age	Otolith section age
Females (N = 290)						
Fork length	0.912	0.969	0.956	0.766	0.862	0.819
Otolith section age	0.947	0.859	0.788	0.938	0.917	
Whole otolith age	0.925	0.893	0.837	0.901		
Otolith thickness	0.930	0.843	0.778			
Otolith width	0.893	0.948				
Otolith length	0.940					
Males (N = 246)						
Fork length	0.895	0.971	0.959	0.815	0.835	0.769
Otolith section age	0.938	0.807	0.710	0.905	0.907	
Whole otolith age	0.923	0.885	0.778	0.846		
Otolith thickness	0.903	0.778	0.725			
Otolith width	0.857	0.778				
Otolith length	0.922					

length and the interaction variables compensate for these changes in the pattern of otolith weight in the multiple regression models of fish age.

The multiple regression models relating fish age with otolith data were fitted with both whole otolith age and otolith section age as dependent variables. Independent variables included in the whole otolith age models, their coefficients, and significance levels are presented in Table 3. All coefficients were highly significant and the models explain 88.1% of the variation in age for females and 92.0% for males, as measured by the coefficient of determination, R^2. Residuals from the models by age category show no trend up to age 35 for females and age 30 for males, after which there is a trend of increasing positive deviation with increasing age. The ages included in this part of the model, however, represented only 7.7% of female and 8.6% of male *S. diploproa* and are therefore not of great concern. These deviations are positive, however, suggesting that the model predictions may relate to otolith growth patterns which are more indicative of otolith section ages.

Variables included in the otolith section age models, their coefficients, standard errors, and significance levels are presented in Table 4. Again, all coefficients are highly significant, but the coefficients of determination are slightly less, explaining 86.1% of the variation in age for females and 85.0% for males. Mean residuals for the different age categories show no significant trend with age.

The model based upon whole otolith ages suffers from inaccuracies in the older ages, where otolith section ages are much greater than whole otolith ages. This is demonstrated in the trend of increasing residuals with increasing age. The model based upon otolith section age, however, is characterized by slightly lower multiple correlation coefficients (Table 4). This may be a result of inaccuracies in estimates of otolith section age of younger fish, where greater difficulty in age de-

TABLE 3.—Regression coefficients and associated statistics on the multiple regression models of whole otolith age for *Sebastes diploproa*.

Variable	Coefficient	SE	P
Females (N = 290)			
Otolith weight	0.1343	0.0091	<0.001
(Otolith weight)^3	-0.107×10^{-6}	0.14×10^{-7}	<0.001
Otolith width	−2.558	0.571	<0.001
Constant (a)	6.4303	3.004	0.033
SD = 4.15			
Multiple correlation, R = 0.939			
Males (N = 246)			
Otolith weight	0.2179	0.0145	<0.001
(Otolith weight)^3	-0.1945×10^{-6}	0.14×10^{-7}	<0.001
Otolith width	−3.4542	0.3942	<0.001
Otolith weight/length	−1.0997	0.2402	<0.001
Constant (a)	16.2572	2.2186	<0.001
SD = 2.797			
Multiple correlation, R = 0.959			

TABLE 4.—Regression coefficients and associated statistics on the multiple regression models of otolith section age for *Sebastes diploproa*.

Variable	Coefficient	SE	P
Females (N = 290)			
Otolith weight	0.2270	0.0137	<0.001
(Otolith width)^2	−0.3288	0.0377	<0.001
(Otolith weight)^3	-0.1134×10^{-6}	0.155×10^{-7}	<0.001
(Otolith length)^2	−0.1114	0.0205	<0.001
Constant (a)	5.0243	1.2982	<0.001
SD = 4.232			
Multiple correlation, R = 0.928			
Males (N = 246)			
Otolith weight	0.2496	0.0158	<0.001
Otolith width^3	−5.7233	0.6949	<0.001
(Otolith weight)^3	-0.1315×10^{-6}	0.266×10^{-7}	<0.001
(Otolith length)^2	−0.0882	0.0256	<0.001
Constant (a)	23.540	3.3823	<0.001
SD = 4.620			
Multiple correlation, R = 0.922			

termination exists with sections. For this reason, I also constructed a hybrid multiple regression model based upon a combination of otolith section and whole otolith ages. The decision on which age to use was arbitrary in the following way: If the difference (otolith section age minus whole otolith age) was ≤5 yr, whole otolith age was chosen; if the difference was >5 yr, otolith section age was chosen. The resulting models are described in Table 5. Independent variables similar to those in the other two models were chosen, and the multiple correlation coefficients were greater in each case.

To analyze the precision of the models, subsamples of 50 male and 50 female *S. diploproa* were taken from the remaining samples not used in the calibration subsample. Lengths and ages were representative of the respective ranges in the overall collection. Ranges of whole otolith age, NMFS age (that from the other agency), and otolith section age in these samples were 2-50, 3-49, and 2-75 for females and 3-34, 4-25, and 3-84 for males, respectively.

Whole otolith age was predicted based upon the appropriate whole otolith age models. Values of estimated age, whole otolith age, and NMFS age as a function of length are plotted in Figure 4. The deviation of NMFS age from whole otolith age increases with increasing length for both males and females. Deviations from the first whole otolith age are presented in Figure 5. Model-induced variability is the difference between estimated whole otolith age and whole otolith age; between-agency variability is whole otolith age minus NMFS age; within-agency variability is the difference of two successive age determinations by the same reader. Mean values of these sources of variation are presented in Table 6 for females and Table 7 for males. In both cases, the mean between-agency variability is greater than either model-induced or within-agency variability. One-way ANOVA demonstrates a significant difference among the three sources (Tables 6, 7). Multiple range testing (least significant difference, $\alpha = 0.05$), moreover, demonstrates that the means are significantly different for both females and males; the range tests suggest that within-agency and model-induced variability are equal and are both significantly less than the between-agency variability.

Only a single otolith section age was determined for specimens from the 1980 confirmation subsample. Ages were estimated from the multiple regression model of section age (Table 4) and compared with conventionally determined section age

TABLE 5.—Regression coefficients and associated statistics on the multiple regression models of age in *Sebastes diploproa*. The ages used for the calibration of these models are based upon either whole otoliths or otolith sections as described in the text.

Variable	Coefficient	SE	P
Females ($N = 290$)			
Otolith weight	0.2233	0.0135	<0.001
(Otolith width)^2	−0.2983	0.0403	<0.001
(Otolith weight)^3	-0.1244×10^{-6}	0.1685×10^{-7}	<0.001
Otolith length	−2.495	0.5084	<0.001
Constant (a)	17.7993	3.7339	<0.001
SD = 4.3967			
Multiple correlation, $R = 0.962$			
Males ($N = 246$)			
Otolith weight	0.2504	0.0157	<0.001
(Otolith width)^2	−0.3598	0.0549	<0.001
(Otolith weight)^3	-0.1272×10^{-6}	0.2800×10^{-7}	<0.001
Otolith length	−2.4123	0.6071	<0.001
Constant (a)	16.6069	3.9145	<0.001
SD = 4.7479			
Multiple correlation, $R = 0.958$			

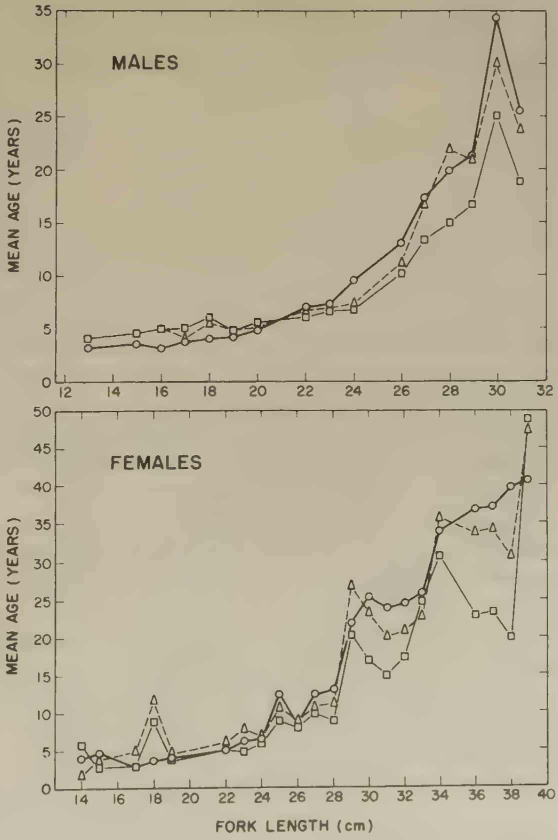

FIGURE 4.—Comparisons of mean whole otolith ages at length for the confirmation subsample of *Sebastes diploproa*. Triangles represent age from reader A, circles the age estimated by the model, and squares the age determined by another laboratory.

TABLE 6.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes diploproa* females. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, within reader variability.

Source	df	Sum of squares	Mean squares	*F*	*P*
Analysis of variance					
Between groups	2	707.77	353.89	23.14	<0.001
Within groups	147	2,247.93	15.29		
Total	149	2,955.70			

Group	*n*	Mean	SD
1	50	4.000	4.686
2	50	−0.51	4.134
3	50	−0.700	2.613

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 3 = Group 2 < Group 1

TABLE 7.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes diploproa* males. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, within reader variability.

Source	df	Sum of squares	Mean squares	*F*	*P*
Analysis of variance					
Between groups	2	207.30	103.65	13.62	<0.001
Within groups	147	1,118.30	7.61		
Total	149	1,325.60			

Group	*n*	Mean	SD
1	50	2.360	3.306
2	50	0.108	2.294
3	50	−0.320	2.575

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 3 = Group 2 < Group 1

(Fig. 6). Ages were close to those predicted from the model with the notable exception of the maximum age for both males and females. In each instance, the maximum ages were greater than the maximum otolith section age in the calibration subsample; the estimated section age is therefore an extrapolation from the model. For the overall subsample, however, the estimated section ages were not significantly different from those determined by conventional methods (paired *t*-test, $\alpha = 0.05$). The observed and predicted ages comparing the confirmation subsample with the predicted ages from the hybrid model are not presented graphically, but the form of the curves for both males and females is virtually identical to that for the section age model (Fig. 6).

Sebastes pinniger

Sebastes pinniger were collected from lat. 43°11′ to 49°26′N at depths from 58 to 375 m (Fig. 7).

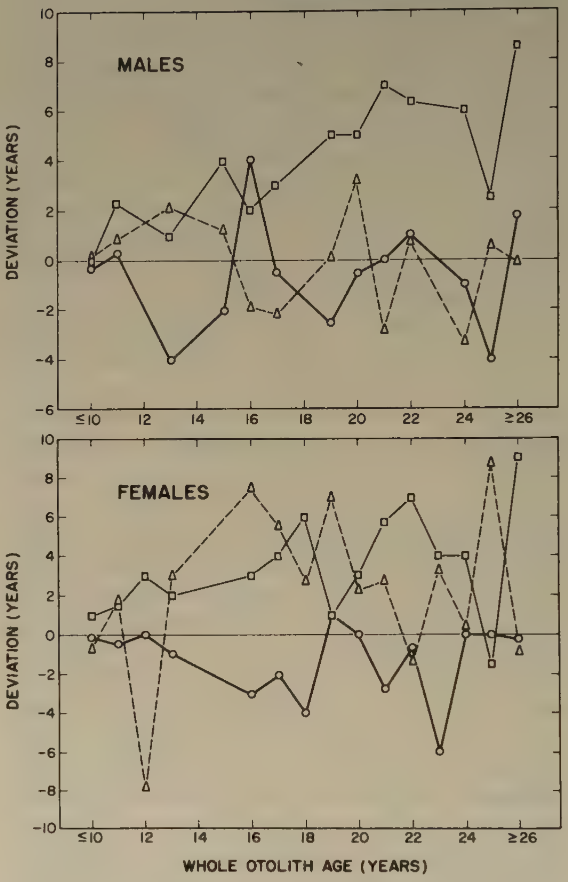

FIGURE 5.—Mean deviations of whole otolith ages from the confirmation subsample of *Sebastes diploproa*. Triangles represent model-induced variability, circles within-agency variability, and squares between-agency variability.

Pairs of otoliths from a total of 519 male and 369 female specimens were taken from the survey. Length frequencies for *S. pinniger* show a mode at 50 cm for males and 52 cm for females. Age frequencies of the entire sample (based upon whole otoliths) demonstrate a mode for both males and females at 12 to 13 yr. Whole otolith ages from the collections ranged from 2 to 25 for males and 2 to 22 for females.

Subsampling every third pair of otoliths from the whole collection resulted in 171 male and 121 female specimens of *S. pinniger*. Again, this subsample was representative of the latitudinal distribution, age range, and length range of the whole sample. Capture, otolith, and age data from these specimens are summarized in Table 8. Otolith section ages in larger fish are generally greater than whole otolith ages, but not to the

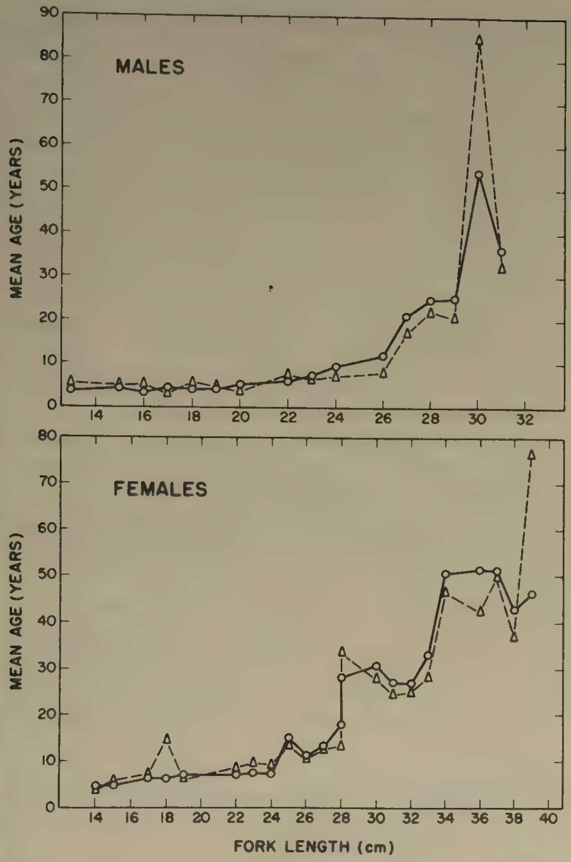

FIGURE 6.—Comparisons of mean otolith section ages at length from the confirmation subsample of *Sebastes diploproa*. Triangles represent otolith section age and circles the model estimated section age.

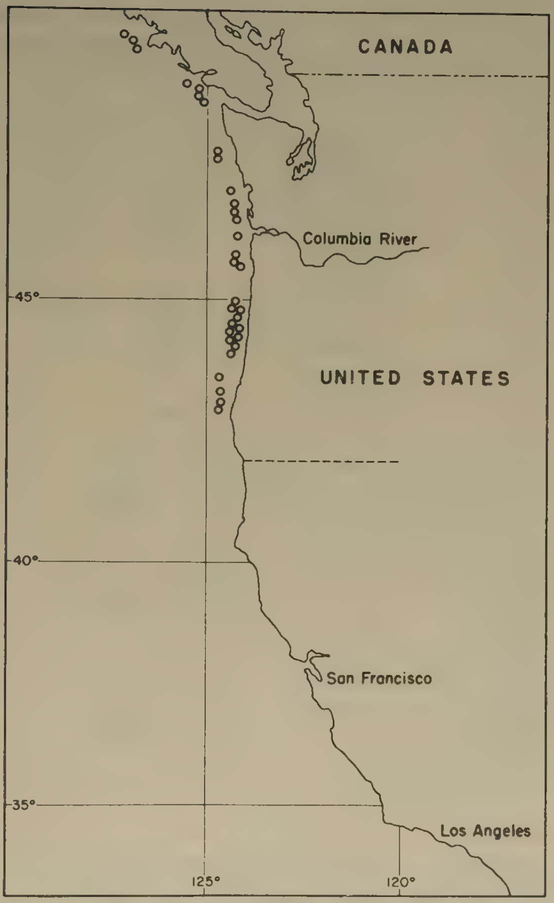

FIGURE 7.—Locations of 1980 West Coast Survey collections from which otoliths of *Sebastes pinniger* were taken for the current study. Samples from the FV *Pat San Marie* and the FV *Mary Lou* are included.

TABLE 8.—Summary of biological and otolith data from the subsampled groups of *Sebastes pinniger* used in developing the age models.

	Females (N = 121)				Males (N = 171)			
Variable	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Depth of capture (fathoms)	32	100	69.8	12.66	37	103	73.3	14.39
Fork length (mm)	152	610	497.8	69.25	170	579	481.64	64.20
Otolith length (mm)	8.00	23.40	19.62	2.27	8.59	22.89	19.56	2.31
Otolith width (mm)	4.45	12.02	9.60	1.06	4.69	11.07	9.46	1.01
Otolith thickness (mm)	0.83	2.01	1.54	0.19	0.79	2.41	1.64	0.29
Otolith dry weight (mg)	53	821	486.7	135.5	58	867	517.0	160.69
Whole otolith age (yr)	2	19	12.4	3.16	2	25	13.2	3.79
Otolith section age (yr)	2	33	14.83	5.09	2	54	20.02	9.77

extent seen for *S. diploproa*. Otolith weight is again an exponential function of length, particularly for males. For females, however, this relationship was nearly linear. Of the ages determined in the calibration subsample, otolith weight has the strongest linear association with whole otolith age for females and whole otolith age and section age for males (Table 9).

The multiple regression models constructed to predict whole otolith age were based upon fewer variables than for *S. diploproa*, but included variables were highly significant (Table 10). The coeffi-

TABLE 9.—Correlation matrix for selected otolith morphometric, weight, and age data for the calibration subsample of *Sebastes pinniger*.

	Otolith weight	Otolith length	Otolith width	Otolith thickness	Whole otolith age	Otolith section age
Females (N = 121)						
Fork length	0.915	0.948	0.923	0.779	0.895	0.755
Otolith section age	0.825	0.735	0.757	0.718	0.795	
Whole otolith age	0.890	0.887	0.851	0.756		
Otolith thickness	0.826	0.765	0.756			
Otolith width	0.920	0.902				
Otolith length	0.917					
Males (N = 171)						
Fork length	0.844	0.940	0.909	0.754	0.847	0.682
Otolith section age	0.898	0.694	0.696	0.883	0.809	
Whole otolith age	0.892	0.837	0.815	0.830		
Otolith thickness	0.910	0.769	0.750			
Otolith width	0.869	0.901				
Otolith length	0.879					

TABLE 10.—Regression coefficients and associated statistics on the multiple regression models of whole otolith age for *Sebastes pinniger*.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith length)^3	0.00095	0.00011	<0.001
(Otolith width)^2	0.0448	0.0126	0.001
SD = 1.30			
Multiple correlation, R = 0.913			
Males (N = 171)			
Otolith weight	0.0280	0.00214	<0.001
(Otolith weight)^3	-0.845×10^{-8}	0.241×10^{-8}	0.001
SD = 1.665			
Multiple correlation, R = 0.900			

cient of determination (R^2) suggests that the models of whole otolith age explain 83.4% of the variation in age for females and 81.0% for males. For both males and females, the constant in the regression was not significantly different from zero and was not included in the models. The residuals from the models show no distinct trend with the exception of a slight increase at ages >17 yr for males; this included 11.1% of the sample.

The variables included in the otolith section age models, their coefficients, standard errors, and significance levels are presented in Table 11. As in the whole otolith age models, there are fewer variables included than for *S. diploproa*; for the male section age model, for example, there is only one variable and the constant included for prediction of age. All variables are highly significant and the coefficients of determination suggest that the otolith section models explain 70.2% of the variation in age for females and 84.6% for males. Mean residuals show a strong trend of increase at ages past 26 yr for male otolith section age models; this represented 23% of the sample.

A model incorporating both otolith section age and whole otolith age was developed using the same criteria for age as in *S. diploproa*. These models were based upon more independent variables but were not significantly better (as based upon the coefficient of determination) than the otolith section models (Table 12). Based upon the multiple correlation coefficients, the best models for *S. pinniger* would be the hybrid model for males and the whole otolith model for females.

For analyzing the precision of the models, sub-

TABLE 11.—Regression coefficients and associated statistics on the multiple regression models of otolith section age for *Sebastes pinniger*.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith weight)^2	0.272×10^{-4}	0.382×10^{-5}	<0.001
Otolith width	0.8368	0.4586	0.071
SD = 2.80			
Multiple correlation, R = 0.838			
Males (N = 171)			
(Otolith weight)^2	0.546×10^{-4}	0.179×10^{-5}	<0.001
Constant (a)	4.0297	0.6022	<0.001
SD = 3.85			
Multiple correlation, R = 0.920			

TABLE 12.—Regression coefficients and associated statistics on the multiple regression models of age in *Sebastes pinniger*. The ages used for the calibration of these models are based upon either whole otoliths or otolith sections as described in the text.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith weight)^2	0.2621×10^{-4}	0.4518×10^{-5}	0.001
(Otolith width)^3	0.4038×10^{-2}	0.2186×10^{-2}	0.067
Constant (a)	3.2137	1.1296	0.005
SD = 2.8239			
Multiple correlation, R = 0.840			
Males (N = 171)			
(Otolith weight)^2	0.1306×10^{-3}	0.2359×10^{-4}	<0.001
(Otolith length)^3	-0.2044×10^{-2}	0.5456×10^{-3}	<0.001
(Otolith weight)^3	-0.6026×10^{-7}	0.2197×10^{-7}	0.007
Otolith length/width	9.7349	4.1381	0.020
Constant (a)	−12.8239	7.4064	0.085
SD = 3.9989			
Multiple correlation, R = 0.924			

samples of 50 male and 50 female *S. pinniger* were taken from the remaining 1980 samples not used in the calibration subsample. These subsamples were representative of the length and age ranges in the overall collection. Ranges of whole otolith age, NMFS age, and otolith section age in these subsamples were 4-26, 4-25, and 4-29 for females and 7-35, 7-32, and 8-45 for males, respectively.

Whole otolith age was estimated from the appropriate whole otolith age model for males and females. Values of model estimated age, whole otolith age, and NMFS age as a function of length are plotted in Figure 8. Female *S. pinniger* ages are similar for all three age determination methods. For males, model-estimated age is similar to the whole otolith age but both are less than the NMFS age (Fig. 8). Deviations from the whole otolith age by the otolith reader whose ages were used to calibrate the model are shown in Figure 9.

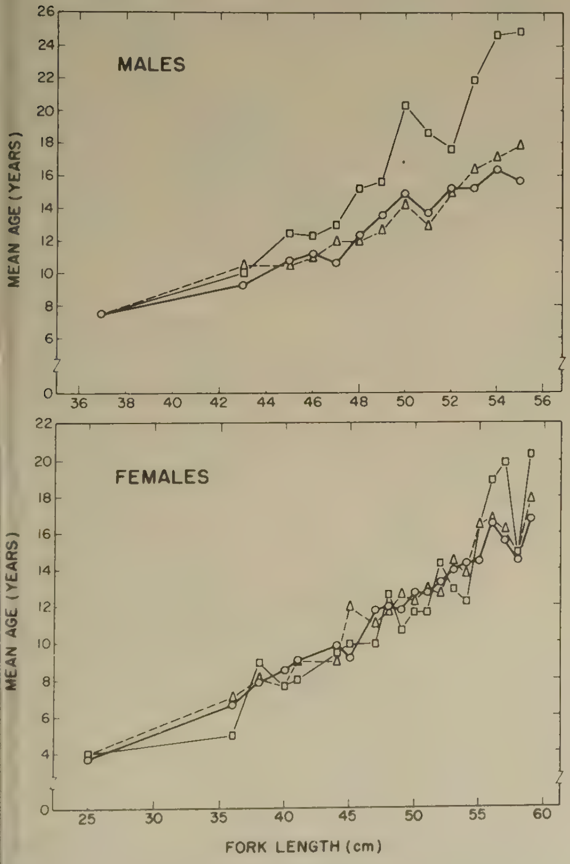

FIGURE 8.—Comparisons of mean whole otolith ages at length from the confirmation subsample of *Sebastes pinniger*. Triangles represent age from reader B, circles the age estimated by the model, squares the age determined by another laboratory.

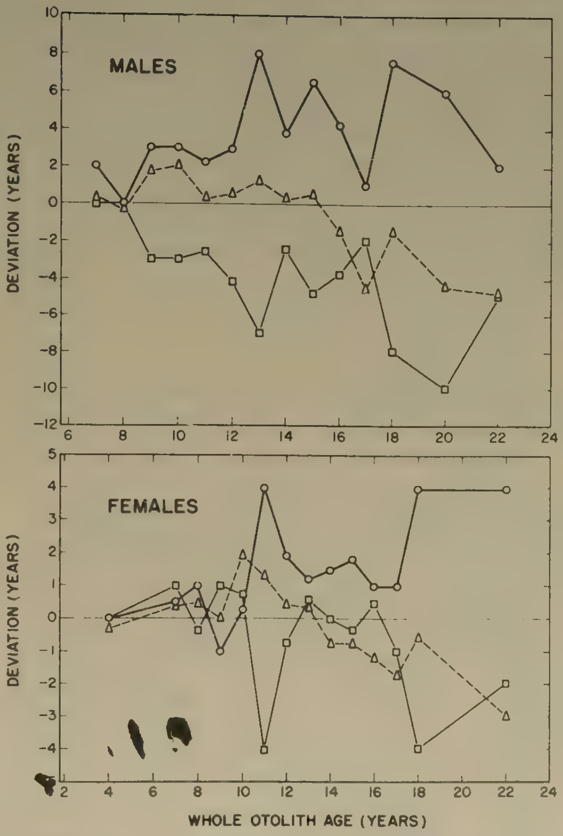

FIGURE 9.—Mean deviations of whole otolith ages from the confirmation subsample of *Sebastes pinniger*. Triangles represent model-induced variability, circles within-agency variability, and squares between-agency variability.

The explanation of these deviations is the same as for *S. diploproa* with the exception that the within-agency variability is a between-reader rather than a within-reader variability. One-way ANOVA within these deviations shows significant differences among the groups for both females (Table 13) and males (Table 14). Multiple range testing (least significant difference, $\alpha = 0.05$) demonstrates that for females, mean between-agency variability and model-induced variability are equal but are both less than within-agency variability (for *S. pinniger* this was based upon two different readers). For males, between-agency variability is less than model-induced variability which is less than within-agency variability. For the purposes of this comparison, however, the model-induced variability is significantly closer to zero than either of the other sources of variability (Table 14).

In the confirmation subsample, section ages estimated from the multiple regression model are

TABLE 13.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes pinniger* females. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, between reader variability.

Source	df	Sum of squares	Mean squares	*F*	*P*
Analysis of variance					
Between groups	2	88.69	44.34	8.67	<0.001
Within groups	147	751.84	5.11		
Total	149	840.53			

Group	*n*	Mean	SD
1	50	−0.320	2.817
2	50	−0.021	1.516
3	50	1.44	2.260

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 1 = Group 2 < Group 3

TABLE 14.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes pinniger* males. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, between reader variability.

Source	df	Sum of squares	Mean squares	*F*	*P*
Analysis of variance					
Between groups	2	1,840.42	920.21	67.43	<0.001
Within groups	147	2,006.21	13.65		
Total	149	3,846.63			

Group	*n*	Mean	SD
1	50	−4.280	4.427
2	50	−0.111	2.107
3	50	4.300	4.112

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 1 < Group 2 < Group 3

compared with conventional section ages in Figure 10. The two ages are similar and as a whole are not significantly different for females but are significantly different for males (paired *t*-test, $\alpha = 0.05$). This is presumably a result of the consistently overestimated otolith section age for *S. pinniger* males. The ages estimated from the hybrid model (Fig. 11) are not significantly different from those determined by the appropriate conventional age (paired *t*-test, $\alpha = 0.05$).

DISCUSSION

The results of this research demonstrate the potential for using objective criteria and multivariate models to determine age in fast- and slow-growing members of the genus *Sebastes*. Past studies have used weight of the eye lens for estimates of age in fishes, amphibians, and certain mammals (Crivelli 1980; Malcolm and Brooks 1981). In fishes, however, this technique is only good for fast-growing species and provides poor estimates of age after several years when length at age becomes highly variable (Crivelli 1980); the same problems exist in estimating age from modal lengths. Growth of most body parts, including the eye lens, is allometric with length rather than age. Growth of the otolith, however, as described above, is a complex function of age as well as length. After a certain size is reached, the fish otolith does not increase in length or width, but continues to increase in thickness, and therefore weight, with age (Fig. 3). The increasing thickness is a function of addition of aragonite crystals only on the internal surface of the otolith (Fig. 1).

Similar patterns of otolith growth in length, width, thickness, and weight have been observed

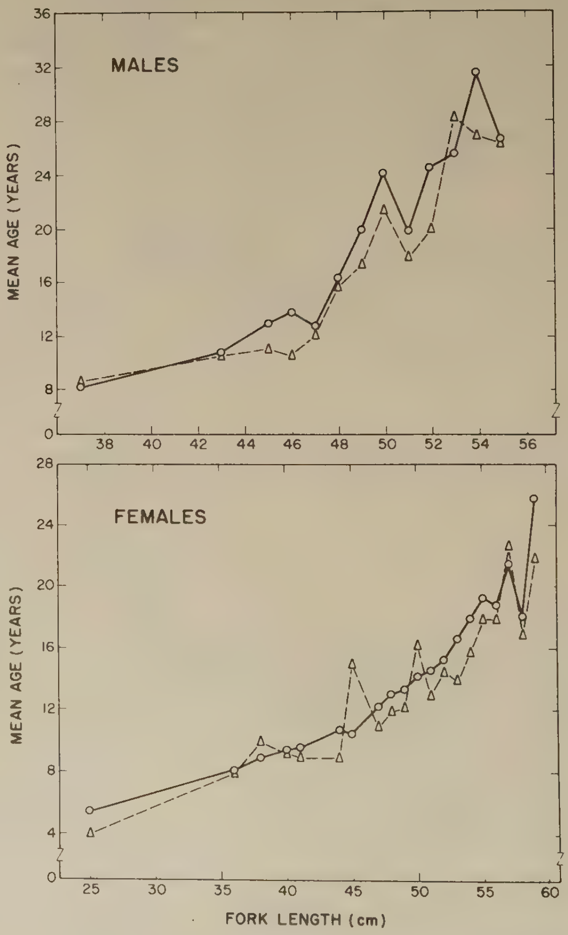

FIGURE 10.—Comparisons of mean otolith section ages at length from the confirmation subsample of *Sebastes pinniger*. Triangles represent otolith section age and circles the model estimated section age.

in other species of fish, but the information has not been applied to the estimation of age, with the exception of preliminary tests using discriminant techniques by Brander (1974). Templeman and Squire (1956), however, noted the importance of this information: "In many fishes, in which accurate age reading is doubtful, otolith weights, which are more factual, may offer a better separation of fish populations than growth rates which are dependent on the judgement of the scale- or otolith-reader." Weight and otolith measurements are valid criteria for age determination based upon the models (Tables 3-5, 10-12) and provide good estimates of age compared with other reading methods (Tables 6, 7, 13, 14; Figs. 4-6, 8-11). Based upon published patterns of otolith growth, these techniques should work for other species of *Sebastes* (Sandeman 1961; Beamish 1979b), Pacific hake (Beamish 1979a), haddock (Templeman and Squire 1956), plaice, sole, turbot, and horse mackerel (Blacker 1974a), and cod (Trout 1954; Blacker 1974a), among others. This technique may therefore be amenable to a wide variety of species of fishes.

Ages determined by scale or otolith readers are generally based on subjective decisions by the age reader, who reads annuli but must distinguish from "false checks", "metamorphic checks", and "spawning checks" (Trout 1961; Bailey et al. 1977). With experience comes reduced individual variability, but aging variability among different otolith readers and especially among different agencies is great; such variability can have important effects upon the estimates of growth parameters important for fisheries management (Sandeman 1961; Brander 1974; Hirschhorn 1974; Kimura et al. 1979). While otolith or scale exchanges are occasionally made between agencies for calibration purposes, this represents additional time spent for gaining greater consistency in ages (Westrheim and Harling 1973; Blacker 1974b), and difficulties may remain if disagreement in aging techniques cannot be resolved. Blacker (1974a) noted that "Recent progress in the use of otoliths for age determination has been limited mainly to the development of new techniques for preparing otoliths for reading and for photography so that aging methods can be readily compared." The techniques described in the present study represent a new approach to the systematic and repeated age determination in species for which continued age determination is necessary; once calibrated and implemented, the models would reduce between-reader and between-agency variability in age determination. Further research, however, should be conducted on variations in the models over seasons, regions, and different years to determine to what extent repeated calibration is necessary.

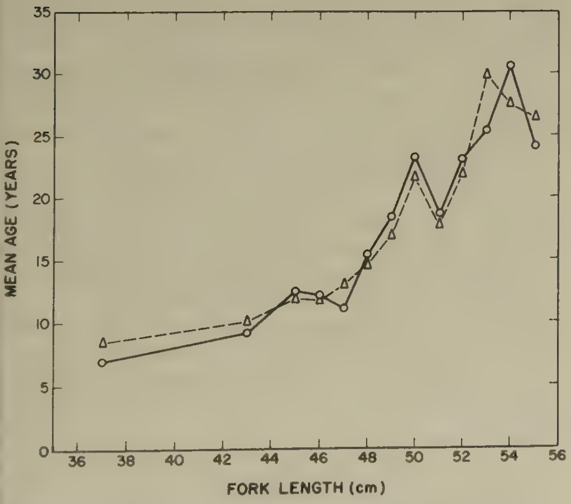

FIGURE 11.—Comparison of ages determined from otoliths and those predicted by the hybrid regression model for *Sebastes pinniger* males. Otolith ages were based upon whole otolith ages if the difference between section and whole otolith ages were ≤ 5; otherwise, otolith sections were used. Triangles represent whole otolith or section age and squares the model estimated age.

Ancillary benefits of the proposed methodology include its simplicity. Reliable, repeatable estimates of age require a great deal of experience on the part of an otolith or scale reader using conventional aging methodology (Blacker 1974a). It is often difficult to maintain a staff of trained otolith readers and retraining may require a large time commitment. The techniques described here require no special training, since the criteria (otolith length, otolith width, and otolith dry weight) are objective and can be measured with simple dial calipers and balance. Time expended for age determination by different methods is as follows: An experienced otolith reader averages about 17 ages/h on whole otoliths, but only 6 to 8 ages/h when otolith sections are used due to the additional preparation necessary. An untrained technician, however, can determine the measurements necessary for the model-based age estimates at a rate of about 40 otoliths/h on a long-term basis. Since the criteria for age are measurable, the techniques will be amenable to automation. Several attempts have been made in the past to automate or semiautomate age analysis using imaging systems based upon differential light transmission (Fawell 1974; Mason 1974). These techniques have generally not been implemented, however, due to the subjective and variable nature of the criteria. Implementation of these techniques with automated systems could result in even further savings of time.

Since estimating the age distribution of exploited fish populations remains an important part of fishery biology, new and improved techniques of age determination are desirable. For shorter lived species, length-based methods are proving important (Pauly and David 1981). Age-length keys are also used quite extensively. Sample sizes necessary for accurate age-length keys, however, must be quite large, particularly for long-lived species such as *Sebastes*. In my relatively small calibration subsamples, for example, there are up to 15 age classes in a single 1 cm length interval (Table 15). Considering the maximum age of *S. diploproa* (Bennett et al. 1982), there could potentially be up to 50 age classes in a single length interval if a sufficient sample size were taken. For such species, age-length keys will be difficult to extrapolate meaningfully to the entire population without very large sample sizes, which must accordingly be aged. Similar, but more severe, problems will apply to techniques which attempt to extract growth parameters from length-frequency data for such long-lived species. The techniques developed by Pauly and David (1981) for faster growing species would be complemented by the current technique for slow-growing, difficult-to-age species. Otoliths could be collected by station, sex, and species without regard to size. From each otolith, after calibration of an age model, the available information could include both fish length and age. This approach to length data collection is not new and has been used by the International Pacific Halibut Commission for several years to estimate length (Southward 1962; Quinn et al. 1983). These techniques could therefore streamline not only the collection of otoliths at sea but also the analysis of age in the laboratory.

TABLE 15.—Number of age classes within single 1 cm length intervals from the calibration subsample. N = number of *Sebastes* specimens in the subsample.

Species	Sex	N	Whole otolith age	Otolith section age
S. diploproa	Female	290	14	14
	Male	246	12	14
S. pinniger	Female	121	6	11
	Male	171	9	15

The difficulty in age determination described above and the resulting variability between laboratories may have a negative impact upon accuracy of fishery models, particularly those using cohort or virtual population analysis (Brander 1974; Alverson and Carney 1975). The new methodology can provide significant time and cost savings over conventional methods and also decrease variability in age estimates. Implementation of these aging techniques, however, will require careful calibration with ages determined by a consensus of expert otolith readers from all management agencies with an interest in each species for which a model is developed.

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LITERATURE CITED

ALVERSON, D. L., AND M. J. CARNEY.
1975. A graphic review of the growth and decay of population cohorts. J. Cons. Int. Explor. Mer 36:133-143.

BAILEY, R. F. J., K. W. ABLE, AND W. C. LEGGETT.
1977. Evidence for the presence of a metamorphic check in capelin (*Mallotus villosus*) otoliths and implications for age determination. J. Fish. Res. Board Can. 34:2008-2014.

BEAMISH, R. J.
1979a. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. J. Fish. Res. Board Can. 36:141-151.
1979b. New information on the longevity of the Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can. 36:1395-1400.

BENNETT, J. T., G. W. BOEHLERT, AND K. K. TUREKIAN.
1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) using $^{210}Pb/^{226}Ra$ measurements in otoliths. Mar. Biol. (Berl.) 71:209-215.

BINGEL, F.
1981. Growth of a cod otolith on the crystal level. Meeresforschung 28:212-215.

BLACKER, R. W.
1974a. Recent advances in otolith studies. *In* F. R. Harden Jones (editor), Sea fisheries research, p. 67-90. John Wiley and Sons, N.Y.
1974b. The ICNAF cod otolith photograph exchange scheme. *In* T. B. Bagenal (editor), The ageing of fish, p. 108-113. Unwin Brothers, Ltd., Surrey.

BOEHLERT, G. W.
1980. Size composition, age composition, and growth of the canary rockfish, *Sebastes pinniger*, and the splitnose rockfish, *S. diploproa*, from the 1977 Rockfish survey. Mar. Fish. Rev. 42(3-4):57-63.

BOEHLERT, G. W., AND R. F. KAPPENMAN.
1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. Mar. Ecol. Prog. Ser. 3:1-10.

BRANDER, K.
1974. The effects of age-reading errors on the statistical reliability of marine fishery modelling. *In* T. B. Bagenal (editor), The ageing of fish, p. 181-191. Unwin Brothers, Ltd., Surrey.

CRIVELLI, A.
1980. The eye lens weight and age in the common carp, *Cyprinus carpio* L. J. Fish Biol. 16:469-473.

FAWELL, J. K.
1974. The use of image analysis in the ageing of fish. *In* T. B. Bagenal (editor), The ageing of fish, p. 103-107. Unwin Brothers, Ltd., Surrey.

GUNDERSON, D. R., AND T. M. SAMPLE.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42(3-4):2-16.

HIRSCHHORN, G.
1974. The effect of different age ranges on estimated Bertalanffy growth parameters in three fishes and one mollusk of the northeastern Pacific Ocean. *In* T. B. Bagenal (editor), The ageing of fish, p. 192-199. Unwin Brothers, Ltd., Surrey.

KIMURA, D. K., R. R. MANDAPAT, AND S. L. OXFORD.
1979. Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*), using otoliths. J. Fish. Res. Board Can. 36:377-383.

MALCOLM, J. R. AND R. J. BROOKS.
1981. Eye lens weight and body size as criteria of age in beaver (*Castor canadensis*). Can. J. Zool. 59:1189-1192.

MARALDO, D. C., AND H. R. MACCRIMMON.
1979. Comparison of ageing methods and growth rates for largemouth bass, *Micropterus salmoides* Lacépède, from northern latitudes. Environ. Biol. Fish. 4:263-271.

MASON, J. E.
1974. A semi-automatic machine for counting and measuring circuli on fish scale. *In* T. B. Bagenal (editor), The ageing of fish, p. 87-102. Unwin Brothers, Ltd., Surrey.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1975. Statistical package for the social sciences. 2d ed. McGraw-Hill, N.Y., 675 p.

PAULY, D., AND N. DAVID.
1981. ELEFAN I, a basic program for the objective extraction of growth parameters from length frequency data. Meeresforschung 28:205-211.

POWER, G.
1978. Fish population structure in Arctic lakes. J. Fish. Res. Board Can. 35:53-59.

QUINN, T. J., II, E. A. BEST, L. BIJSTERVELD, AND I. R. MCGREGOR.
1983. Sampling Pacific halibut (*Hippoglossus stenolepis*) landings for age composition: History, evaluation, and estimation. Int. Pac. Halibut Comm. Sci. Rep. 68, 56 p.

SANDEMAN, E. J.
1961. A contribution to the problem of age determination and growth-rate in *Sebastes*. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 150:276-284.
1969. Age determination and growth rate in redfish, *Sebastes* sp., from selected areas around Newfoundland. Int. Comm. Northwest Atl. Fish. Res. Bull. 6:79-106.

SIX, L. D., AND H. F. HORTON.
1977. Analysis of age determination methods for yellowtail rockfish, canary rockfish, and black rockfish off Oregon. Fish. Bull., U.S. 75:405-414.

SOUTHWARD, G. M.
1962. A method of calculating body lengths from otolith measurements for Pacific halibut and its application to portlock-albatross grounds data between 1935 and 1957. J. Fish. Res. Board Can. 19:339-362.

TEMPLEMAN, W., AND H. J. SQUIRE.
1956. Relationship of otolith lengths and weights in the haddock *Melanogrammus aeglefinis* (L.) to the rate of growth of the fish. J. Fish. Res. Board Can. 13:467-487.

TROUT, G. C.
1954. Otolith growth of the Barnets Sea cod. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 136:89-102.
1961. The otolith of group-0 *Sebastes mentella* Travin. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 150:297-299.

WESTRHEIM, S. J., AND W. R. HARLING.
1973. Report on the 1972 comparison of Pacific ocean perch otolith and scale interpretations. Fish. Res. Board Can. Manuscr. Rep. Ser. 1259, 24 p.

WILLIAMS, T., AND B. C. BEDFORD.
1974. The use of otoliths for age determination. *In* T. B. Bagenal (editor), The ageing of fish, p. 114-123. Unwin Brothers, Ltd., Surrey.

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Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasi*

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Abstract

Fishes inhabiting estuaries, rivers, and embayments are subject to turbid conditions. Larvae of many fishes utilize estuaries as nursery areas. For visual plankton feeders such as larval fishes, turbidity may reduce search and reaction distances, resulting in lowered feeding abilities. In this study feeding Pacific herring larvae, *Clupea harengus pallasi,* were exposed to suspensions of estuarine sediment and Mount Saint Helens volcanic ash at concentrations ranging from 0 mg · l^{-1} to 8 000 mg · l^{-1}. In all experiments, maximum feeding incidence and intensity occurred at levels of suspension of either 500 mg · l^{-1} or 1 000 mg · l^{-1} with values significantly greater than controls (0 mg · l^{-1}). Feeding decreased at greater concentrations. The suspensions may enhance feeding by providing visual contrast of prey items on the small perceptive scale used by the larvae. Larval residence in turbid environments such as estuaries may serve to reduce predation from larger, visual planktivores, while searching ability in the small larval perceptive field is not decreased.

Introduction

Estuaries serve as important nursery areas for the larvae of a wide variety of fishes. Many species inhabit estuaries when turbidity is high, and indeed some species have been shown to prefer turbid conditions, at least as juveniles (Blaber & Blaber, 1980). Larval fishes, particularly at first feeding, require high food densities and have relatively poor searching capabilities (Hunter, 1972, 1981). While zooplankton densities may occur at high levels within estuaries (Heinle & Flemer, 1975), turbidity may result in suboptimal feeding conditions for larvae. The effects of turbidity on feeding, however, have not been determined for larval fishes.

Growth and survival of lake herring larvae *(Coregonus)* are not influenced by suspended sediments at low, naturally occurring concentrations (1–28 mg · l^{-1}) (Swenson & Matson, 1976). At higher concentrations, short term exposures to suspended sediment increase larval mortality (Auld & Schubel, 1978; Rosenthal, 1971; Sherk *et al.*, 1975). Turbidities greater than 100 mg · l^{-1} may occur in estuarine areas, particularly during tidal currents (Auld & Schubel, 1978).

Large-scale mortalities often occur among captive larvae immediately following yolk absorption, implicating starvation as a major cause of death. Appropriately sized food particles must be present in high concentrations for significant survival and growth (Rosenthal & Hempel, 1970; Hunter, 1972). Although Swenson & Matson (1976) noted no effects of low turbidity on feeding of larval lake herring, greater turbidity decreases feeding rates in juvenile bluegill (Gardner, 1981), most likely through decreased prey availability (Vinyard & O'Brien, 1976). Differences exist, however, between feeding behavior in larval and juvenile stages of fishes. Larvae are visual feeders with small search volumes; small larvae (3–5 mm) typically feed on particles about 0.050 mm wide (Hunter, 1981). In addition to lowered prey availability, larvae may

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consume suspended particles with food. This could result in blockage of the esophagus, preventing or hindering first feeding, as noted by Rosenthal (1971).

In this paper we report the effects of turbidity on feeding abilities of early larvae of the Pacific herring, *Clupea harengus pallasi*, a species which spawns in estuaries. Spawning occurs in Oregon and Washington estuaries in January through early May (Steinfeld, 1972; Pearcy & Meyers, 1974). Larvae remain in the estuarine nursery grounds through the juvenile stage. The estuary is commonly turbid during their residence, suggesting that feeding in turbid water is common for this species.

Methods

Two types of sediment suspensions were used in the experiments. Estuarine sediment was collected at low tide from mudflats in Yaquina Bay, Oregon. Volcanic ash from Mount Saint Helens was obtained from airfall ash at Moses Lake, Washington. This ash was dominated (weight percent fraction) by 0.020-0.045 mm particles (Fruchter *et al.*, 1980). Both sediment and volcanic ash were standardized with respect to size by settling techniques. Particles larger than 0.024 mm were removed by settling over 10 cm. Particles remaining in suspension were allowed to settle over 48 h. After this time, the ash and sediment were treated differently. For both, the supernatant was siphoned off the settled material. For the volcanic ash, the remaining material was dried and the ash subsequently dispersed. The sediment was autoclaved and maintained in a liquified state to maintain particle separation; this solution typically contained about 80% water. Final particle sizes of volcanic ash and estuarine sediment were analyzed with a Coulter counter (Table 1). This particle distribution allowed maintenance of suspensions with the relatively low turbulence necessary for larval fishes; for flow-through systems larger particles would have clogged the screens necessary to segregate the larvae. Secondly, the smaller particles may be more realistic with respect to what herring larvae may encounter in estuaries. Standardized suspensions (mg · l^{-1}) of sediment and ash were used to develop calibration curves of optical density; these curves were used to check the concentrations of suspensions during experiments.

Table 1. Particle size distribution of volcanic ash and estuarine sediment after settling and preparation for egg and larval experiments.

Particle size μ	Sediment		Ash	
	% by number	% by weight	% by number	% by weight
19.0-23.9	0.1	3.9	0.1	3.8
15.1-19.0	0.3	8.0	0.6	8.7
12.0-15.1	1.0	12.1	2.9	18.8
9.5-12.0	2.4	14.3	6.0	21.4
7.5- 9.5	5.0	15.1	10.5	18.4
6.0- 7.5	9.9	15.1	14.6	12.9
4.8- 6.0	19.2	14.6	18.9	8.3
3.8- 4.8	29.5	11.0	21.8	4.9
3.0- 3.8	32.7	6.0	24.6	2.8

The spectral absorbance characteristics of ash and sediment suspensions were determined on a Beckman DU-6 spectrophotometer with samples in a cuvette with a 1-cm light path. At equivalent concentrations, light is more highly attenuated in sediment suspensions than in volcanic ash suspensions (Fig. 1). Volcanic ash, moreover, shows a flat spectral absorbance curve, as one might expect from the glassy, crystalline nature of the ash (Fruchter *et al.*, 1980). The absorbance of the estuarine sediment is heavily skewed towards shorter wavelengths.

All experiments were conducted at the Oregon State University Marine Science Center. The seawater system for these facilities draws water from Yaquina Bay during high tides to maintain salinities in excess of 27 g · l^{-1}. For experimental use, the water was passed through a sand and gravel filter to remove particulate matter and then irradiated with ultraviolet light to eliminate pathogens. It was mixed with the appropriate amount of dechlorinated fresh water to bring the final salinity to 15 g · l^{-1}, and held in a large aerated reservoir in a constant temperature room to allow equilibration to the desired temperature. Light in the constant temperature room, where all experiments were conducted, was maintained at an intensity of 80 ft-c at the water surface of experimental vessels; photoperiod was adjusted to reflect seasonal changes in day length.

Pacific herring spawn in Yaquina Bay during winter and early spring months. All work was conducted with naturally spawned eggs collected along

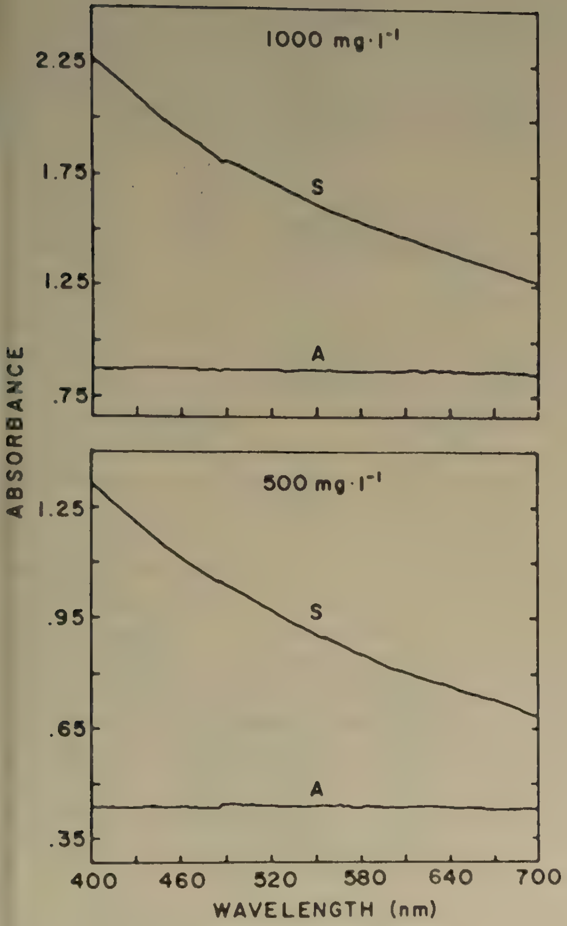

Fig. 1. Spectral absorbance characteristics and attenuation of visible light over a 1-cm light path for two concentrations of estuarine sediment (S) and volcanic ash (A). At equivalent concentrations, the solutions differ in both spectral absorbance and optical density.

the north jetty of Yaquina Bay on 6 March and 14 April 1982. After bringing the eggs to the laboratory, they were placed in static 40 l aquaria with aeration at 10 ° C in a constant temperature laboratory. Approximately 50% of the water was changed daily. As larvae hatched, they were moved to 250 l tanks prior to use in experiments. Larvae used for feeding experiments were monitored for yolk utilization and feeding ability. When specimens were capable of feeding, the rotifer *Brachionus plicatilis,* along with algal culture, was added to the tanks in densities which allowed a high rate of feeding.

Larval feeding experiments were conducted with the prey source consisting of the rotifer, *B. plicatilis.* Methods of mass culture of the rotifer followed Theilacker & McMaster (1971). The marine planktonic alga, *Isochrysis* sp. (Ewart & Epifanio, 1981), was cultured as food for the rotifers. The average size of *Brachionus* was 0.220 mm long and 0.125 mm wide, a size acceptable to first feeding herring larvae. Rotifers were harvested for experiments by sieving through a 0.065 mm screen, washed in clean seawater, and placed in a larger vessel with algae overnight to acclimate to the 10 ° C experimental temperature.

Two types of experiments were conducted with feeding larvae. The first was based upon experiments which minimized turbulence and disturbance to the larvae during feeding trials. First-feeding clupeoid larvae are visual feeders with stereotyped behavioral sequences necessary for feeding (Hunter, 1972; Blaxter & Staines, 1971). Therefore the excessive disturbance necessary for constant maintenance of given suspensions might inhibit feeding capabilities, resulting in very low feeding incidence even in controls. The two types of experiment were therefore based upon periodic suspension of ash or sediment in the first set and constant maintenance of the suspensions in the second set. This latter set of experiments resulted in higher turbulence but maintained mean suspension concentrations within 10% of the nominal value; thus lower feeding incidence was expected *a priori.*

The first set of experiments was conducted in 10-l black circular tanks containing a total volume of 5 l during the experiments. Larvae were chosen at times when all had initiated feeding; experiments were run on 24 and 25 March with larvae aged 10 days posthatching (mean notochord length 8.7 mm). On the night prior to the experiment, 100 to 200 larvae were introduced into 3 l of water in the experimental vessel without food to allow evacuation of stomach contents. Preliminary experiments demonstrated that evacuation of identifiable food items occurred overnight. The following morning, an additional 2 l of suspended ash or sediment was added to make final concentrations of 0, 500, 1 000, 2 000, 4 000, and 8 000 mg · l⁻¹. The prey *(B. plicatilis)* was then added, followed by thorough stirring with a paddle, to begin the experiments. Food concentrations of six rotifers per milliliter initiated a well-defined feeding response in the larvae. The duration of the experiment was 2 h with resuspension of ash or sediment concentrations at 15 min intervals. While this treatment kept turbulence low, it also resulted in some loss of suspension concentration. Separate trials were conducted to determine the change in suspension concentration at the surface, middle, and bottom of the experimental vessel at the end of the 15 min stirring interval. Monitoring the concentrations showed that the surface layer (top 0.5 cm) densities decreased, averaging 32% lower than the nominal concentrations. In the middle depth, there was an average 16% decrease in concentration, and at the bottom of the containers, a 50% increase in concentration. A similar trend of changes in the densities of food organisms was apparent, with increasing abundance of food particles in the denser ash or sediment at the bottom of the experimental vessels at the end of 15 min. Experiments were terminated after 2 h by quickly sieving the suspensions and larvae through a 0.335 mm nylon screen and immediately preserving the larvae in 10% Formalin to minimize regurgitation of food. These experiments were run in duplicate.

In the feeding experiments with continual suspension, an apparatus was designed to eliminate the need for manual suspensions of sediments and to maintain more uniform exposure of the suspensions. The device (Fig. 2) allowed testing of three replicate groups of larvae. Three 1-l experimental chambers were cut from 10 cm (i.d.) black ABS plastic pipe covered at one end with 0.335 mm nylon mesh screen and connected in a rosette pattern to a center polyvinyl chloride pipe which supported both the chambers and an airlift device. The rosette was partially submerged in a round 10 l black plastic tank containing the suspension of ash or sediment which was kept in suspension outside the chambers by a variable-speed stirrer. The nylon screen was small enough to contain the larvae and still allow suspensions and rotifers to be recycled back into the 10 l container. A concave deflector helped to create a mixing area within the larger container. Two airstones placed beneath each center pipe airlifted the suspensions through three glass tubes (9 mm i.d.) which penetrated a rubber stopper within the center pipe. These glass tubes were bent at right angles at the top and directed into the three dosing chambers. The airlift system above the test containers was continued with 1.3 cm (o.d.) plastic tubing with three 3.6 mm holes bored along one side to allow control of the volume of suspensions entering the test containers. Flow rates were maintained at approximately 240 ml min^{-1}. In these experiments, larvae aged 22 days posthatching (mean notochord length 10.0 mm) were used. Three replicates of about 20 larvae were tested per treatment, in which the suspensions were continually maintained. Again, larvae were preserved at the termination of experiments for later enumeration of feeding incidence and number of food particles.

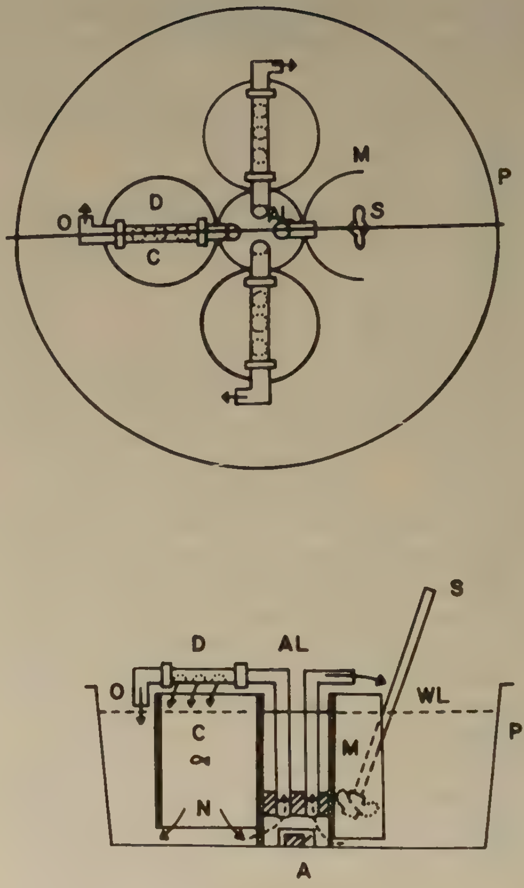

Fig. 2. The experimental apparatus used to maintain continuous suspensions of sediment or volcanic ash. Total volume of each container holding larvae was 1 l; the volume of the larger tank was 10 l. Flow rate into the smaller containers was maintained at approximately 240 ml/min. A, airstone. AL, airlift system. C, dosing chamber. D, flow regulator. M, mixing area. N, 0.335 mm nylon screen. O, overflow. P, 10 l tank. S, stirrer connected to variable speed motor. WL, water level. Arrows indicate the direction of flow of suspension through the apparatus.

Preserved larvae were examined individually under a dissecing microscope for presence of food. This could be done without dissection as the gut is straight in herring larvae and the transparent gut wall makes observation possible (Checkley, 1982).

Results

The herring larvae used in all experiments readily fed upon *B. plicatilis.* A total of 1 502 larvae were examined from the volcanic ash suspension feeding experiments and 1 272 from the estuarine sediment feeding experiments, with an overall average of 69% and 74%, respectively, of the larvae feeding during the 2-h duration of the experiment. In both sets of experiments, the percentage of larvae feeding increased dramatically from the control experiments to 500 and 1 000 mg · l^{-1} before showing a gradual decline with successive increases in sediment or ash concentrations to near that of the controls at 8 000 mg · l^{-1} (Fig. 3). In the ash suspensions, control larvae each consumed approximately 10 *Brachionus* whereas larvae at 500 mg · l^{-1} consumed showed the maximum number, nearly 17. Values declined until those at 8 000 mg · l^{-1} were near those of the controls (Fig. 4A). A similar pattern is seen for sediment suspensions (Fig. 4B). There was greater feeding incidence by larvae in sediment suspensions than in volcanic ash suspensions at concentrations in excess of 500 mg · l^{-1}. The effect of sediment on the number of prey ingested per larva was not significantly different (Wilcoxon matched-pairs signed-rank test, $P > 0.05$) from that of ash.

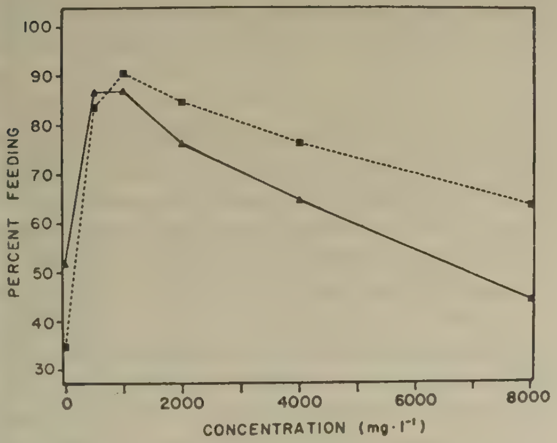

Fig. 3. Effects of periodically suspended estuarine sediment and volcanic ash upon the feeding success (percent feeding) of larval Pacific herring. Larvae were allowed to evacuate guts overnight; experiments were of 2-h duration with 6 *Brachionus* per milliliter in the suspensions. Solutions were uniformly resuspended by stirring every 15 min during the feeding period. Values are means of two replicates. Dashed line, estuarine sediment. Solid line, volcanic ash.

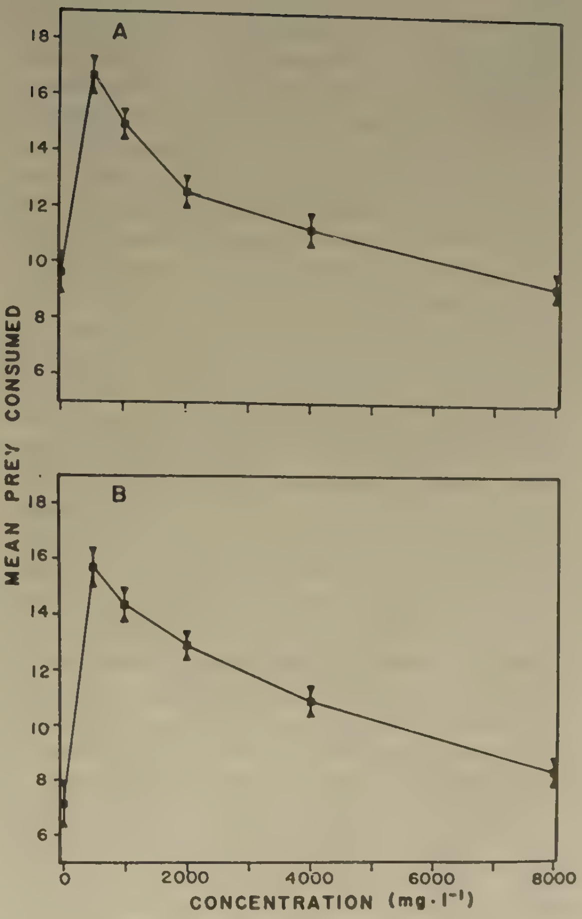

Fig. 4. Effect of periodic resuspensions upon the feeding success (prey consumed per feeding larva) in larval Pacific herring. Error bars indicate ±1 standard error. Numbers of feeding larvae range from 54 to 259. A, Volcanic ash. B, Estuarine sediment.

Results from these semistatic feeding trials suggest that both sediment and volcanic ash stimulate feeding incidence and activity as compared to control fish. In these trials, the settlement of the suspended particles between stirring lowered the effective suspension concentration in the tanks by the values described in the previous section. Swenson & Matson (1976) noted that larval lake herring swim up the water column in response to suspended sediment. This may have occurred in these experiments as well, resulting in increased visibility of prey organisms in the near surface water of the test container with its lower concentration of suspension.

In the second set of experiments, suspensions remained within 10% of the nominal value during the course of the experiment. Feeding incidence was lower, averaging 31% for ash and 23% for sediment over all concentrations. As a function of concentration, the curves of feeding incidence for ash and sediment were not significantly different but showed a different trend from the semistatic experiments (Fig. 5). The percentage of larvae feeding was again initially greater than in the controls, but then decreased with increasing suspension concentration, reaching nearly zero at 4 000 mg · l^{-1} for sediment. In these experiments the variability in the numbers of *Brachionus* consumed per larva within experiments as well as within replicates was high (Fig. 6A, B), suggesting significant variability among individuals.

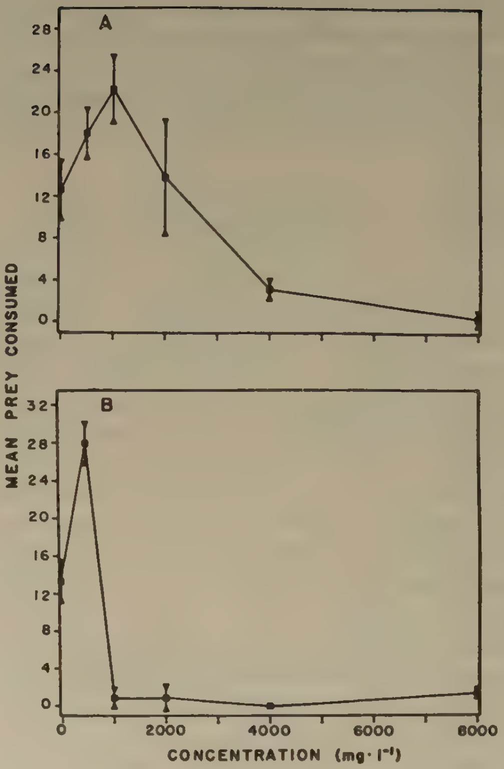

Fig. 6. Effects of continuous suspensions on the feeding success (prey consumed per feeding larva) in larval Pacific herring. Error bars indicate ±1 standard error. Numbers of feeding larvae ranged from 0 to 42. A, Volcanic ash. B, Estuarine sediment.

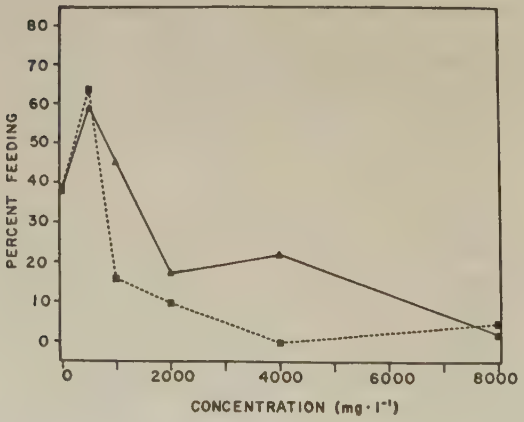

Fig. 5. Effects of continuous suspensions of estuarine sediment and volcanic ash upon the feeding success of larval Pacific herring. Larvae were allowed to evacuate guts overnight; experiments were of 2 h duration with 6 *Brachionus* per milliliter in the suspensions. Values are the means of three replicates. Dashed line, estuarine sediment. Solid line, volcanic ash.

With increasing turbidity, number of *Brachionus* consumed also increased to a maximum at 1 000 mg · l^{-1} in the ash experiments (Fig. 6A) and at 500 mg · l^{-1} in the sediment experiments (Fig. 6B). In the sediment experiments, feeding at 1 000 mg · l^{-1} and higher was nearly zero. Equivalent values in volcanic ash were not reached until a concentration of 8 000 mg · l^{-1}; values in volcanic ash suspensions greater than 500 mg · l^{-1} were significantly greater than in sediment (Wilcoxon matched-pairs signed-rank test, $P < 0.05$). The differences between the semistatic and dynamic feeding trials may be due either to the decreasing concentrations of sediment or ash in the upper levels of the semistatic tank in the intervals between stirring or to the greater turbulence in the dynamic experiments. In the dynamic trials, despite a turnover of 25% of the water in the experimental vessel per minute, larvae were clearly able to feed in lower concentrations of both ash and sediment (Figs. 5, 6A, B). While feeding incidence was gen-

Table 2. Presence of ash or sediment in guts of larval herring from the feeding trials conducted 11 and 13 May, 1982. From each concentration, 20 larvae were examined.

Suspension concentration (mg l)	% incidence in larval guts	
	Volcanic ash	Estuarine sediment
0	0	0
500	95%	100%
1000	70%	80%
2000	50%	40%
4000	30%	50%
8000	25%	50%

erally lower than in semistatic experiments, the mean number of prey consumed per feeding larva was greater in the dynamic experiments for the controls and concentrations of 500, 1000, and 2 000 mg · l^{-1} in the ash suspensions (Figs. 4A, 6A) but only in the controls and 500 mg · l^{-1} in the sediment suspensions (Figs. 4B, 6B). This difference, however, probably reflects the greater age of larvae in the dynamic experiments. We thus interpret the continued feeding by the larvae in the semistatic experiments at suspension concentrations greater than 2 000 mg · l^{-1} in ash and greater than 1 000 mg · l^{-1} in sediment to be a result of the decreasing concentration in the surface of the tank and possibly the behavioral movement of the larvae to this level as well.

In the feeding trials, sediment and ash were taken into the gut in limited amounts. From the dynamic feeding experiments, groups of 20 larvae from each concentration were examined for presence or absence of ash or sediment in the intestine and also qualitatively for amount. Generally, with increased concentration of the suspension (beyond the control), the incidence of particles in the gut decreased (Table 2). Only in the highest concentration (8 000 mg · l^{-1}) of both ash and sediment, were some individuals present with large amounts in the gut. Generally, only traces of ash or sediment were apparent. The observation of the greatest incidence at the lowest suspension concentration would support the contention that ingestion of ash or sediment was associated with feeding, since feeding incidence was also highest at these concentrations (Figs. 3, 5).

Discussion

Oviparous fishes which produce large numbers of small eggs suffer high mortality rates in early life history stages, mostly from starvation and predation (Hunter, 1976). Environmental pollution may further increase mortalities through either direct effects (Longwell & Hughes, 1981; Hunter *et al.*, 1979, 1981) or indirect effects (Rosenthal & Alderdice, 1976).

The effects of sediment on reproduction and early life stages of warmwater fishes have recently been reviewed by Muncy *et al.* (1979). A variety of effects, dependent upon species and type of sediment, is apparent. For eggs, the most consistent effect appears to be the reduction in respiratory gas exchange. Early larvae depend upon epidermis for respiratory gas exchange (Hunter, 1972; Weihs, 1980) thus a coating of particulates may hinder gas exchange. The epidermis in early larvae, furthermore, is only a few cells thick (O'Connell, 1981; Jones *et al.*, 1966), making larvae subject to abrasion damage and other potentially sublethal effects (Boehlert, 1984).

A priori, one would expect suspended particulates to affect larval fish feeding. First-feeding larvae are very small, have relatively small perceptive fields, and possess only weak swimming abilities; early larvae are thus able to search only limited volumes for food. Blaxter & Staines (1971) showed that larval Atlantic herring, *Clupea harengus harengus*, the same age as those in the present study (10 and 22 days posthatching) searched only 0.2 to 0.5 l per h. Compounding low search volume is a low feeding success rate, estimated to range from 10 to 30% (Blaxter & Staines, 1971). Thus, based upon feeding success rate and volume searched it is obvious that first-feeding larvae require relatively high densities of food particles to survive. Laboratory studies of food density and its effect on feeding and survival confirm that very high densities are required. Experimental food densities for 50% survival range from 199 l^{-1} for sea bream (Houde, 1978) to 4 000 l^{-1} (northern anchovy, O'Connell & Raymond, 1970).

For larvae to locate these high densities of food, visual orientation is critical; increased turbidity or other factors affecting visual field and perception may reduce food consumption and increase the probability of starvation. Gardner (1981) noted reduced feeding rates in juvenile bluegill exposed to bentonite clay concentrations of 400 to 1 200 mg · l⁻¹; he observed no change, however, in size selectivity of available prey. Similarly, Moore & Moore (1976) suggested that increased turbidity reduced the ability of flounder to see epi-, benthic prey, resulting in longer times for prey capture. Our results are thus unexpected. In both semistatic and continual suspensions of both estuarine sediment and volcanic ash, low suspension levels actually increased feeding rates (Figs. 4A, B; 6A, B) and the percentage of larvae feeding (Figs. 3, 5). Similar results were observed in filter feeding copepod, *Eurytemora affinis;* feeding rates were enhanced at 100 mg · l⁻¹ of Fuller's earth, but maximum ingestion rate decreased at particulate levels in excess of 250 mg · l⁻¹ (Sherk *et al.*, 1975).

We suggest two possible mechanisms for enhanced feeding in sediment and ash suspensions. First, particulates may enhance visual contrast allowing larvae to better visualize their prey. In the controls, feeding incidence and the numbers of particles consumed per feeding larva were low; in these black-walled containers, however, feeding was nonetheless higher than in preliminary control experiments with glass-walled containers. Confer & Blades (1975) and Confer *et al.* (1978) suggested that planktivorous fishes have greater reaction distances for more heavily pigmented prey. Similarly, the relatively transparent *Brachionus* may have been contrasted against the background of the suspensions. Based upon the spectral absorbance of the two solutions (Fig. 1), the sediment may have provided the greater contrast. A second explanation is based upon light scattering. In turbid water, particle scattering will disperse light in all directions. Thus *Brachionus* will be illuminated from all directions, possibly decreasing its transparency.

No great differences were apparent between ash and sediment for the larval feeding experiments. The lower concentrations of both ash and sediment resulted in enhanced feeding. In the dynamic experiments (Fig. 5), the feeding incidence was greatest at 500 mg · l⁻¹ for sediment and rapidly decreased thereafter, whereas the peak for volcanic ash was at 1 000 mg · l⁻¹ and decreased less markedly. Light transmission through equivalent suspensions of ash and sediment differ, with significantly greater light transmission through the volcanic ash (Fig. 1). For visual feeders such as fish larvae, this difference in available light may cause the difference in feeding abilities. The spectral absorbance differences (Fig. 1) may also have played a role. Larval herring have only single cones in the retina (Blaxter & Jones, 1967). Blaxter (1968) used behavioral measures to suggest three maxima (450, 520, and 600 nm) of photopic visual sensitivity in larval Atlantic herring. Action spectra for feeding on *Balanus* and *Artemia* nauplii, however, were dominated by wavelengths near 500–600 nm. At these longer wavelengths absorbance differences of equivalent concentrations of volcanic ash and sediment are less (Fig. 1).

A comparison of the present data with that of Gardner (1981) and Moore & Moore (1976) suggests that prey density and perceptive field may both play a role. Herring larvae 10 to 20 days old have a perceptive distance of only 3.5 mm (Blaxter & Staines, 1971). In both of the past studies, larger fish, with correspondingly larger perceptive fields, were used; Vinyard & O'Brien (1976) and Confer *et al.* (1978) suggested that turbidity reduces the reaction distance for feeding. With our study, it is therefore probable that the greater feeding incidence in suspensions of 500–1 000 mg · l⁻¹ would be diminished with decreasing prey density and encounter rate. In nature, however, Doan (1941) suggested that turbidity might increase the abundance of microcrustaceans at the surface, resulting in enhanced larval feeding.

Another effect of turbidity-induced light reduction may be a change in the vertical distribution of larvae. This may have a great effect on larvae in estuaries, where vertical distribution may have important effects upon horizontal distribution. Swenson & Matson (1976) observed a change in larval vertical distribution within test suspensions of sediment. We noted similar effects in the semistatic feeding experiments despite increased densities of *Brachionus* in the bottom of the tanks. Larval fishes generally use light intensity for depth regulation (Blaxter, 1974). Thus light attenuation from higher than normal turbidity may result in larvae occupying shallower depths. In estuarine fish larvae such as herring, depth regulation may be necessary to maintain populations within an estuary (Weinstein *et al.*, 1980). This has been observed in larvae of Atlantic herring (Graham, 1972) and is probably true of Pacific herring as well. A distribution higher in the water column could therefore result in advection out of the estuary and probable increases in mortality.

A possible benefit of larval fish residence in moderately turbid estuaries with lower light levels may be reduced predation pressure. Howick & O'Brien (1983) noted that prey behavior and motion is an important component of predator success. It is thus conceivable that larval herring reduce feeding activity under high light levels (low turbidity), and that the observed feeding pattern is behaviorally determined. This is not supported, however, by behavioral observations; although Blaxter (1973) suggested that larval herring are active at the surface at night, the activity was associated with vertical migration and not feeding. Instead, we feel that visual contrast or light scattering may explain our results. Ritchie (1972) suggested that turbidity reduced the ability of fish to locate prey but also decreased predation pressure. The decreased feeding capabilities of larger planktivorous fishes in turbid conditions (Vinyard & O'Brien, 1976; Gardner, 1981) are a function of the limitation of visual field, as discussed earlier. Thus, in turbid conditions, if larvae are able to maintain high feeding rates, their advantage increases. Blaber & Blaber (1980) suggested that turbidity was the most important factor affecting juvenile fish abundance in estuaries, with highest fish abundance during highest turbidity levels; moreover, where a gradient of turbidity existed, fish abundance was highest in the most turbid waters. Natural sediment suspension concentrations may reach some 100 mg · l^{-1} in estuaries (Auld & Schubel, 1978). It would thus be interesting to use suspension concentrations between 0 and 500 mg · l^{-1} to determine if a lower optimum level exists for larval herring. The increased feeding capabilities, however, certainly occur within environmentally realistic suspension concentrations.

Summary

Larval Pacific herring are able to feed at a greater rate under moderate suspensions of fine-grained sediment and volcanic ash than under clear-water control conditions; this ability decreases with increasing suspension level. Two mechanisms are suggested to account for the enhancement of feeding over controls. First, we suggest that in the small visual field of the larvae, contrast is enhanced by the background provided by the sediment particles. Secondly, the particles scatter light in all directions, possibly resulting in greater illumination of the food particles, which in turn can decrease the transparency of the food particles. Feeding abilities of the larval herring are thus adapted to residence in the turbid estuarine environments occupied during the larval stage.

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References

Auld, A. H. & J. H. Schubel, 1978. Effects of suspended sediment on fish eggs and larvae: a laboratory assessment. Estuar. Coast. mar. Sci. 6: 153–164.

Blaber, S. J. M. & T. G. Blaber, 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish Biol. 17: 143–162.

Blaxter, J. H. S., 1968. Visual tresholds and spectral sensitivity of herring larvae. J. exp. Biol. 48: 39–53.

Blaxter, J. H. S., 1973. Monitoring the vertical movements and light responses of herring and plaice larvae. J. mar. biol. Ass. U.K. 53: 635–647.

Blaxter, J. H. S., 1974. The eyes of larval fish. In M. A. Ali (ed.), Vision in Fishes. Plenum Press, N.Y.: 427–443.

Blaxter, J. H. S. & M. P. Jones, 1967. The development of the retina and retinomotor responses of the herring. J. mar. biol. Ass. U.K. 47: 677–697.

Blaxter, J. H. S. & M. E. Staines, 1971. Food searching potential in marine fish larvae. In D. J. Crisp (ed.), 4th Europ. mar. Biol. Symp. Cambridge Univ. Press, Cambridge: 467–485.

Boehlert, G. W., 1984 in press. Abrasive effects of Mt. St. Helens ash upon epidermis of yolk-sac larvae of Pacific herring, *Clupea harengus pallasi*. Mar. envir. Res. 12: 113–126.

Checkley, D. M., 1982. Selective feeding by Atlantic herring *Clupea harengus* larvae on zooplankton in natural assemblages. Mar. Ecol. Prog. Ser. 9: 245–253.

Confer, J. L. & P. I. Blades, 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571–579.

Confer, J. L., G. L. Howick, M. H. Corzette, S. L. Kramer, S. Fitzgibbon & R. Landesberg, 1978. Visual predation by planktivores. Oikos 31: 27–37.

Doan, K. H., 1941. Relation of sauger catch to turbidity in Lake Erie. Ohio J. Sci. 41: 449-452.

Ewart, J. W. & C. E. Epifanio, 1981. A tropical flagellate food for larval and juvenile oysters, *(Crassostrea virginica)* Gmelin. Aquaculture 22: 297-300.

Fruchter, J. S., D. E. Robertson, J. C. Evans, K. B. Olsen, E. A. Lepel, J. C. Laul, K. H. Abel, R. W. Sanders, P. D. Jackson, N. W. Wogman, R. W. Perkins, H. H. Van Tuyl, R. H. Beauchamp, J. W. Shade, J. L. Daniel, R. L. Erikson, G. A. Sehmel, R. N. Less, A. V. Robinson, O. R. Moss, J. K. Briant & W. C. Cannon, 1980. Mount St. Helens Ash from the 18 May 1980 eruption: Chemical, physical, mineralogical, and biological properties. Science 209: 1116-1125.

Gardner, M. B., 1981. Effects of turbidity on feeding rates and selectivity of bluegills. Trans. Am. Fish. Soc. 110: 446-450.

Graham, J. J., 1972. Retention of larval herring within the Sheepscot Estuary of Maine. Fish. Bull., U.S. 70: 299-305.

Heinle, D. R. & D. A. Flemer, 1975. Carbon requirements of a population of the estuarine marine copepod *Eurytemora affinis*. Mar. Biol. 31: 235-247.

Houde, E. D., 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. mar. Sci. 28: 395-411.

Howick, G. L. & W. J. O'Brien, 1983. Piscivorous feeding behavior of large mouth bass: An experimental analysis. Trans. Am. Fish. Soc. 112: 508-516.

Hunter, J. R., 1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70: 821-838.

Hunter, J. R. (ed.), 1976. Report of a colloquium on larval fish mortality studies and their relation to fishery research. Jan. 1975. NOAA Tech. Rep. NMFS Circ. 395.

Hunter, J. R., 1981. Feeding ecology and predation of marine fish larvae. In R. Lasker (ed.), Marine Fish Larvae. Washington Sea Grant, Seattle: 33-77.

Hunter, J. R., S. E. Kaupp & J. H. Taylor, 1981. Effects of solar and artificial ultraviolet-B radiation on larval northern anchovy, *Engraulis mordax*. Photochem. Photobiol. 34: 477-486.

Hunter, J. R., J. H. Taylor & H. G. Moser, 1979. Effect of ultraviolet irradiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and Pacific mackerel, *Scomber japonicus*, during the embryonic stage. Photochem. Photobiol. 27: 1-14.

Jones, M. P., F. G. T. Holliday & A. E. G. Dunn, 1966. The ultrastructure of the epidermis of larvae of the herring *(Clupea harengus)* in relation to the rearing salinity. J. mar. biol. Ass. U.K. 46: 235-239.

Longwell, A. C. & J. B. Hughes, 1981. Cytologic, cytogenetic, and embryonic state of Atlantic mackerel eggs from surface waters of the New York Bight in relation to pollution. Rapp. P. V. Reun. Cons. Int. Explor. mer 178: 76-78.

Moore, J. W. & I. A. Moore, 1976. The basis of food selection in flounders, *Platichthys flesus* (L.) in the Severn estuary. J. Fish. Biol. 9: 139-156.

Muncy, R. J., G. J. Atchison, R. V. Bulkley, B. W. Menzel, L. G. Perry & R. G. Summerfelt, 1979. Effects of suspended solids and sediment on reproduction and early life of warmwater fishes: A review. U.S. Envir. Prot. Ag. Corvallis, Oregon, 101 pp.

O'Connell, C. P., 1981. Development of organ systems in the northern anchovy, *Engraulis mordax* and other teleosts. Am. Zool. 21: 429-446.

O'Connell, C. P. & L. P. Raymond, 1970. The effect of food density on survival and growth of *Engraulis mordax* (Girard) in the laboratory. J. exp. mar. Biol. Ecol. 5: 187-197.

Pearcy, W. G. & S. S. Myers, 1974. Larval fishes of Yaquina Bay, Oregon; A nursery ground for marine fishes? Fish. Bull., U.S. 72: 201-213.

Ritchie, J. C., 1972. Sediment, fish, and fish habitat. J. Soil Wat. Conserv. 27: 124-125.

Rosenthal, H., 1971. Wirkung von 'Rotschlamm' auf Embryonen und Larven des Herings, *Clupea harengus*. Helgoländer wiss. Meeresunters. 22: 366-376.

Rosenthal, H. & D. F. Alderdice, 1976. Sublethal effects of environmental stressors, natural and pollutional, on marine fish eggs and larvae. J. Fish. Res. Bd Can. 33: 2047-2065.

Rosenthal, H. & G. Hempel, 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.). In J. H. Steele (ed.), Marine Food Chains. Univ. Calif. Press, Berkeley: 344-364.

Sherk, J. A., J. M. O'Connor & D. A. Neumann, 1975. Effects of suspended and deposited sediments on estuarine environments. In L. E. Cronin (ed.), Estuarine Research. Academic Press, N.Y. 2: 541-558.

Steinfeld, J. D., 1972. Distribution of Pacific herring spawn in Yaquina Bay, Oregon, and observations on mortality through hatching. M.S. Thesis, Ore. St. Univ., Corvallis, 75 pp.

Swenson, W. A. & M. L. Matson, 1976. Influence of turbidity on survival, growth, and distribution of larval lake herring *(Coregonus artedii)*. Trans. Am. Fish. Soc. 105: 541-545.

Theilacker, G. H. & M. F. McMaster, 1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. 10: 183-188.

Vinyard, G. L. & W. J. O'Brien, 1976. Effects of light and turbidity on the reactive distance of bluegill *(Lepomis macrochirus)*. J. Fish. Res. Bd Can. 33: 2845-2849.

Weihs, D., 1980. Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, yolk-sac larvae. Fish. Bull., U.S. 78: 109-118.

Weinstein, M. P., S. L. Weiss, R. G. Hodson & L. R. Gerry, 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. Fish. Bull., U.S. 78: 419-436.

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LARVAL AND JUVENILE GROWTH OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, AS DETERMINED FROM OTOLITH INCREMENTS

The black cod or sablefish, *Anoplopoma fimbria*, has been the subject of an intensifying fishery off the west coast of North America over the last decade. Biological information on this species, however, including data on spawning, early life history, age and growth, and population structure, is relatively meager. Sablefish are widely distributed in the northern Pacific, with adults most abundant at depths of 366-915 m (Hart 1973). Mason et al. (1983) suggested that eggs are spawned and developed in waters deeper than 300 m and colder than 6°C off Canada. Juveniles occur in shallow water, however, and larvae are almost exclusively neustonic (Kendall and Clark[1]). Thus larval development and growth occur in much warmer water than that inhabited by later stages, particularly in the southern portion of the species range.

Sablefish growth has been described by Heyamoto (1962) and Pruter (1954), among others, who used scale annuli to define the growth pattern. More recent work, however, has shown that the age estimates, particularly for older, mature fish, are in error; growth is apparently much slower and longevity much greater than previously thought (Beamish and Chilton 1982). The warmer neustonic habitat of the larvae may result in different growth patterns in early life; ontogenetic changes in growth and habitat are relatively common among deeper living fishes (Boehlert 1982; Luczkovich and Olla 1983). The only observations on growth of young sablefish are those of Heyamoto (1962), who suggested that juveniles of 12-16 cm fork length (FL) were about 6 mo old. In the present study we report on the growth of field-collected larval and juvenile sablefish where age was estimated by enumerating growth increments on the otoliths.

Materials and Methods

Larval and juvenile sablefish were collected in 1981-83. Larvae were taken in 0.5 m neuston nets (Sameoto and Jaroszynski 1969) with 0.505 mm mesh, off the coasts of Oregon and Washington during May 1982 by the RV *Poseydon*. Samples were immediately preserved in 80% ethanol. After sorting, larvae were stored in individual vials labeled with sample number and date. Additional larvae were collected with neuston nets in May 1983 by the RV *Ekvator*. Larger juveniles (> 70 mm standard length (SL)) were taken in a small mesh purse seine deployed from 24 to 40 km off of the Oregon-Washington coasts during the summer months of 1981 (Fig. 1). Specimens were frozen on board and held until measurements and otoliths were taken. Fork lengths to the nearest millimeter were recorded for these larger juveniles and standard lengths to the nearest 0.1 mm were measured for all larvae and small juveniles. No corrections were made for potential shrinkage from preservation of young larvae, but alcohol preservation causes no noticeable shrinkage in length of anchovy larvae (Theilacker 1980). For subsequent analysis, fork lengths were converted to standard length by the relationship SL (mm) = 0.91 FL (mm) −1.15 (n = 54, r^2 = 0.999), which was based upon specimens 21.7 to 297 mm FL.

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[1] Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and northern California, April-May 1980. Processed Rep. 82-11, 44 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98102.

Otoliths of larval sablefish were removed and cleaned under a dissecting microscope fitted with polarizing filters. Increments on otoliths from larvae < 26 mm SL were clearly visible from the focus to the margin (Fig. 2); these otoliths were left intact, affixed to microscope slides with histological mounting medium and cover slips, and increments were read in the sagittal plane (see Taubert and Coble 1977 for terminology). For larger larvae and most juveniles, a sagittal section of the otolith provided the clearest increments. The left otolith of every pair was mounted in histological medium on a microscope slide and the

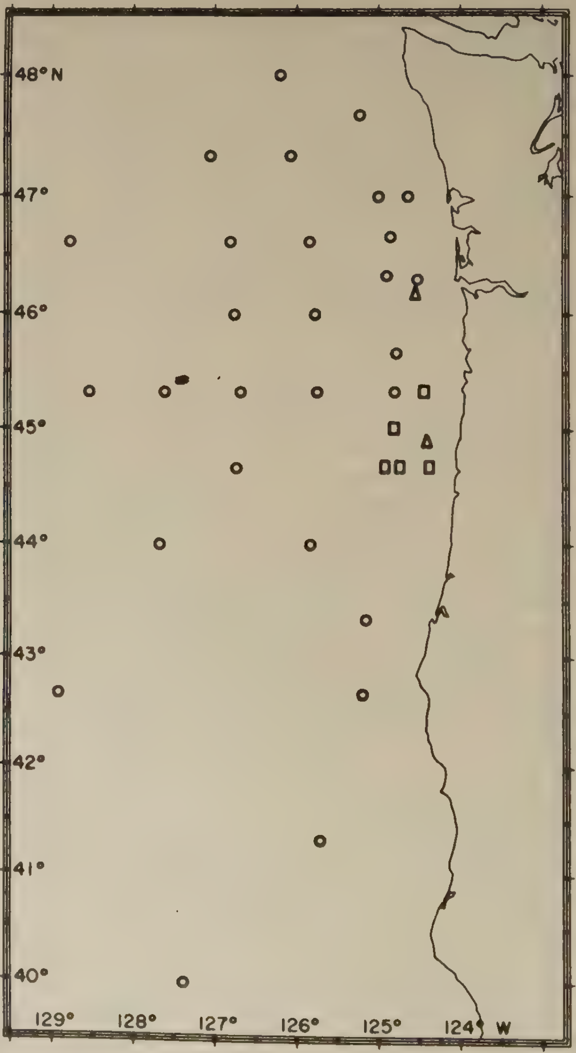

FIGURE 1.–Distribution of *Anoplopoma fimbria* samples, along the Pacific coast, used for age and growth analysis. Circles represent the neuston samples taken during May 1982, triangles represent the purse seine samples taken during summer 1981, and squares represent the 1983 neuston samples.

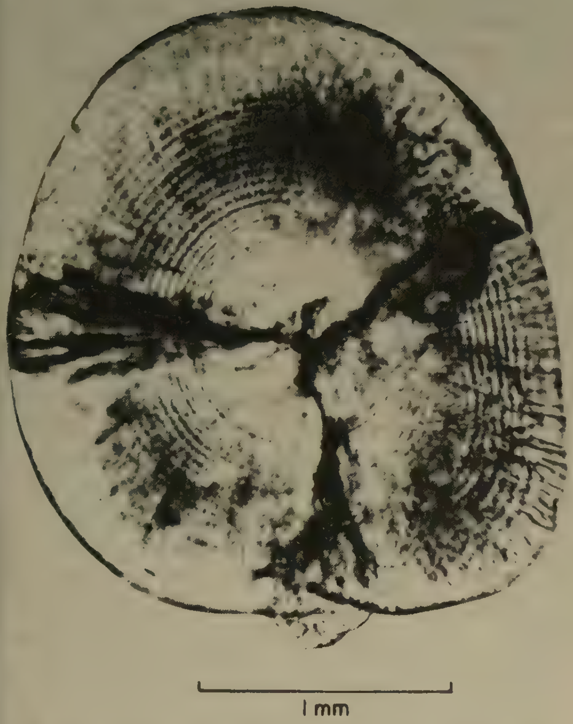

FIGURE 2.–Sagitta otolith from a larval *Anoplopoma fimbria* (22.0 mm SL; duplicate increment counts were 37 and 40 d). Scale bar = 0.1 mm.

internal surface was ground until the focus was visible. The microscope slide was heated and the section was turned over to expose the external surface. Grinding and polishing continued, while care was taken to insure that material was not lost from the margin. The result was a clear, thin section of the otolith in the sagittal plane. For some of the larger juveniles (> 100 mm SL), transverse sections were cut from the otoliths using a diamond saw, mounted on microscope slides, and ground to make the increments clear. All otoliths were read under a compound microscope at 400× or 1,000× magnification. Two independent counts were made for each otolith. These counts were made at least 2 wk apart; the age assigned to each specimen was the mean of the two counts.

Increments, comprised of adjacent light and dark ring pairs, were distinct and clear in the smallest otoliths (Fig. 2), but interpretation became more difficult as the increments became progressively smaller and as changes in growth patterns occurred in the otolith structure of the older specimens. There was no evidence of subdaily patterns in the increments, and each increment was assumed to represent 1 d. Support for the daily deposition of increments was provided by data on three live juvenile sablefish held in the laboratory (Table 1). The specimens were captured by neuston net off Newport, OR, and transported to the laboratory where they were fed to satiation daily on *Artemia*. A check, apparently associated with capture and transfer to the laboratory, was evident on the otolith of each fish. The numbers of increments past this check corresponded closely to days captive; the minor differences are attributed to counting error and/or difficulty in interpretation of the check (Table 1). We thus consider the increments to be deposited with a daily periodicity. Hereafter increment counts will be equated with days after first increment formation; as we discuss later, first increment formation may occur at first feeding.

Data from the 1982-83 larval collections and the 1981 juvenile collections were fitted separately with simple linear regressions. Nonlinear curves (exponential, logistic, and Laird-Gompertz) were fitted to combined data with the NLIN procedure on the SAS[2] statistical package (SAS Institute, Inc. 1982).

TABLE 1.—Growth and increment formation in captive specimens of *Anoplopoma fimbria*. L_1, L_2; standard length (mm) at capture and death, respectively.

Capture date	L_1	L_2	Days captive	Increment past check	Total increments
2 May 1983	19.9	60.4	31	31	63
17 May 1983	14.1	53.4	40	38	95
24 May 1983	53.8	109.7	32	33	87

Results and Discussion

This study considers a total of 105 individuals, including 71 larvae and juveniles (9.8 to 41.2 mm SL) from the 1982 neuston collections, 21 juveniles (102.8 to 259.6 mm SL) from the 1981 purse seine collections, and 13 larvae (10.4 to 25.3 mm SL) taken in the 1983 neuston collections. Mean increment counts ranged from 9 increments for the youngest larva to 180 increments for the oldest juvenile. The abundance of larval sablefish in the neuston (Kendall and Clark footnote 1) at such young ages suggests that larvae move rapidly after hatching from the deep spawning region rather than early growth occurring at depths as suggested by Mason et al. (1983). The difference between the two increment counts for each otolith increased with increasing count, but the coefficient of variation remained the same for the two ranges. For the larvae collected in 1982, with an overall mean of 30.8 increments, the mean difference was 1.67 increments (n = 71, standard deviation (SD) = 1.45). For the 1981 juvenile collections, with overall mean of 109.5 increments, the mean difference between the two estimates was 6.57 increments (n = 21, SD = 5.03).

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Growth rates of field-collected larval and juvenile sablefish differ considerably. The data for the 1982 larval collections is described by the line

$$\mathrm{SL} = 0.375\ (\mathrm{age,\ d}) + 5.27$$
$$n = 71,\ r^2 = 0.838,$$

suggesting a mean growth rate for small larvae of 0.375 mm/d and an intercept of 5.27 mm, which coincides with the size of newly hatched larvae (Mason et al. 1983). Similarly the 1981 juvenile data is described by the line

$$\mathrm{SL} = 1.469\ (\mathrm{age,\ d}) - 0.926$$
$$n = 21,\ r^2 = 0.822,$$

suggesting a mean growth rate of 1.47 mm/d. Certain of these growth differences may have been a function of gear selection. If net avoidance is a function of fish size, as for most other planktonic organisms (Barkley 1972), then the oldest specimens taken in the neuston gear may have been only the slow-growing members of that cohort. Alternatively, interruptions of increment formation, resulting in underestimates of age, may occur. This has been observed for some species by Geffen (1982). In the laboratory specimens, however, one individual (L_2 = 60.4 mm SL, Table 1) ceased eating for 5-6 d, became emaciated, and died. The last five increments near the margin were smaller than the remainder, but the 1:1 correspondence of days to increments suggests that increment formation continued.

Estimated age-at-length data from all years were combined to describe the growth of sablefish to an age of about 200 d. Comparing exponential, logistic, and Laird-Gompertz growth models, the best fit (as judged by residual sums of squares) was provided by the Laird-Gompertz growth model (Fig. 3) in the form:

$$L_t = L_0\ (A_0/\alpha)\ (1 - \exp(-\ \alpha t))$$

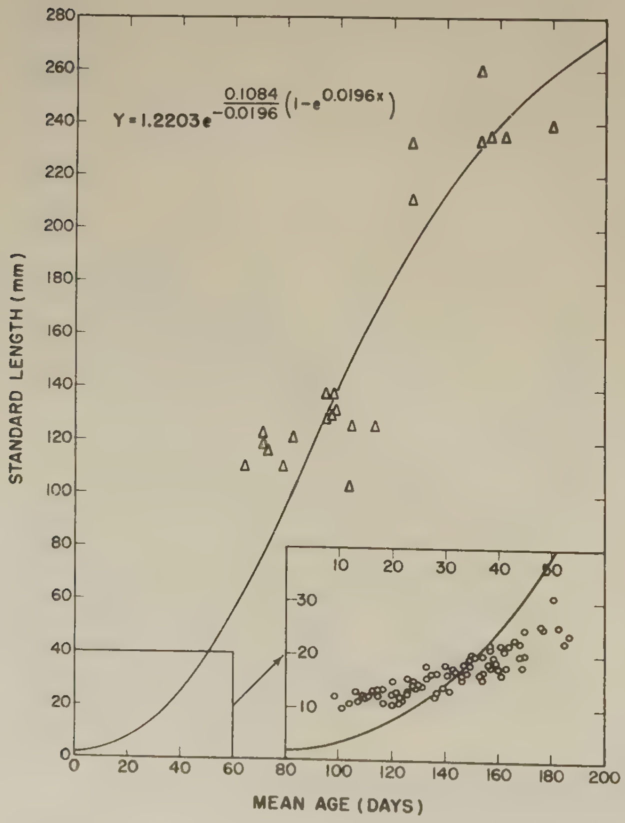

FIGURE 3.–Estimated age at length for all *Anoplopoma fimbria* in the study. Specimens taken in neuston nets (n = 84, including the 13 from 1983) are represented by circles, 1981 juvenile specimens from purse seine collections (n = 21) are represented by triangles. The equation and line represent the least squares fit of the Laird-Gompertz growth model.

where L_t = standard length (mm) at age t (d), L_0 = initial length (y-intercept), and A_0 and α are fitted parameters (Table 2).

This sigmoid curve suggests relatively slow growth to an age of about 50 d and a length of about 25 mm SL, followed by rapidly accelerating growth through the juvenile stage, an inflection point at 113.2 mm, and an asymptotic length near 307.8 mm. Since sablefish achieve lengths to 100 cm (Hart 1973), these results should not be extrapolated beyond the ages in the present study. Also, the predicted fit of zero age individuals (L_0) is 1.22 mm SL (Table 2; Fig. 3). This value does not accurately reflect the length of sablefish at hatching. Egg size in sablefish ranges from 1.8 to 2.2 mm and newly hatched larvae are 5 to 6 mm (Mason et al. 1983). If daily increments are first laid down at first feeding as in some other species (Laroche et al. 1982), then this intercept is clearly an underestimate. Mean egg size suggests a length at first feeding of about 8 mm (Shirota 1970). The smallest larva taken in the present study was 9.8 mm SL (Fig. 3). This part of the curve may be related to the inclusion of the older, slower growing neustonic specimens. Another factor may be effects of shrinkage; small specimens were preserved in ethanol, older juveniles frozen. The magnitude of shrinkage for *A. fimbria* is unknown, but capture and preservation of other fish larvae causes shrinkage which decreases with increasing age or size (Theilacker 1980). Thus increases in actual length for small individuals may have been relatively greater, changing the fitted equation and possibly increasing the length at time zero (Fig. 3).

Heyamoto (1962) estimated growth for young sablefish, suggesting that specimens 12.3 to 16.4 cm FL (11.1 to 14.8 cm SL) were 6 mo old. His data, however, were based upon estimating the age at collection by difference between capture and an assumed spawning season. In our study, 6-mo-old specimens were > 24 cm SL. The specimens captured by Heyamoto (1962) were taken by trawl in 320 to 412 m, much deeper than the epipelagic juveniles in our study. Beamish et al. (1983) used daily increments as part of a study to validate annulus formation in sablefish. In nine specimens 23 to 27 cm FL (208 to 245 mm SL), they observed from 270 to 350 (mean 313) increments but suggested that the fish were 1 yr old due to the inability to count all increments. Based upon our growth curve (Fig. 3), their ages would be overestimates.

TABLE 2.—Fitted parameters of the Laird-Gompertz growth model for larval and juvenile *Anoplopoma fimbria* in the present study. The curve is fitted to all larvae and juveniles (N = 105) based upon counts of otolith increments.

Parameter	Estimate	Asymptotic standard error
L_0	1.2203	0.4675
A_0	0.1084	0.0146
α	0.0196	0.0015

Recent observations of laboratory growth are in substantial agreement with growth described by our curve. Shenker and Olla[3] found average growth rates as high as 2.3 mm/d for juvenile sablefish fed ad libitum. These fish were near the lengths where our curve predicts fastest growth (2 mm/d, Fig. 3). High growth rates were also observed for fish smaller than 25 mm, where our data suggest relatively slow growth. Grover and Olla[4] noted starvation of field-collected sablefish larvae based upon morphological criteria; thus food probably limits sablefish growth in the field. This species apparently has a great scope for growth given high laboratory rations or patches of high prey density in the field.

The distribution of dates of first increment formation were estimated by back calculating from the ages of all specimens in our study. Since larvae and juveniles were from different years and sampling gears, it is possible that differences would be observed in this distribution. Since the plankton gear selects for smaller larvae due to avoidance by later stages, the results could be biased if the entire spawning season were not sampled. The median dates for the 1982 larvae (8 April) and the 1981 juveniles (18 March), however, were similar. Thus all 105 samples were combined and the distribution of the dates of first increment formation plotted (Fig. 4). The distribution has a mode in early April. If the first increment is formed in association with first feeding, as in most other species studied (Brothers et al. 1976; Taubert and Coble 1977; Laroche et al. 1982), then the spawning dates would precede the distribution in Figure 4. Ware (1975) provided an egg size-incubation time relationship for fishes; sablefish, with a 2 mm egg, would have an incubation time of 13 d. If a similar time is spent in yolk absorption before first feeding, peak spawning would occur in early March. This generally agrees with most other reports of the spawning season for *A. fimbria.*

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[3] Shenker, J., and B. L. Olla. Laboratory growth and feeding of juvenile sablefish, *Anoplopoma fimbris.* Unpubl. manuscr.

[4] Grover, J., and B. L. Olla. Field evidence for starvation of larval sablefish, *Anoplopoma fimbria.* Manuscr. in prep. Northwest and Alaska Fisheries Center, Newport Field Office, National Marine Fisheries Service, NOAA, c/o Marine Science Center, Marine Science Drive, Newport, OR 97365 (direct correspondence to B. L. Olla).

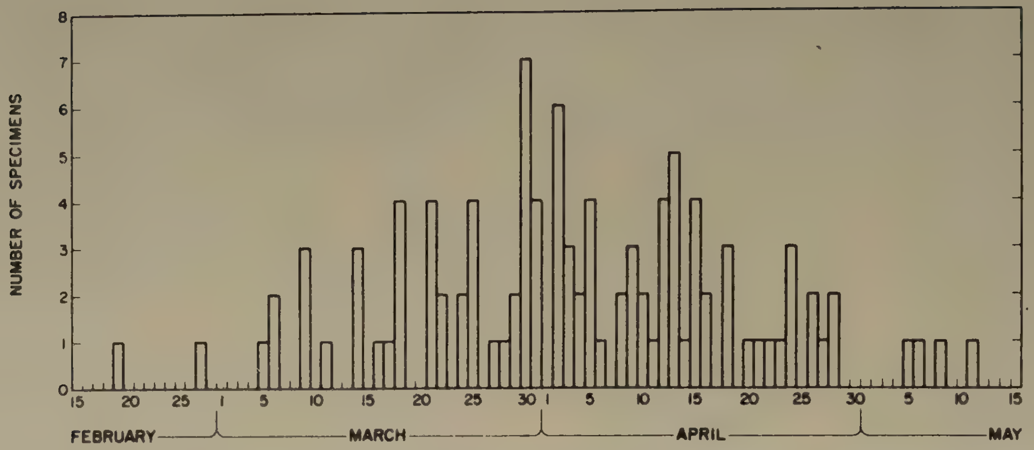

FIGURE 4.–Distribution of dates of first increment formation for *Anoplopoma fimbria*, determined by back-calculations using age and collection date.

Phillips (1958) defined the peak spawning season off California to be January-February. Bell and Gharrett (1945) suggested that the spawning season was around December off Washington based upon fishermen's observations and the presence of spent females in January. Farther north, Thompson (1941) observed ripe females and fertilized eggs in March at Cape St. James (lat. 51°45′N). More recent work has shown that the spawning season off British Columbia occurs in January to February with the peak of spawning in February (Mason et al. 1983).

Our observed growth rates for *A. fimbria* during the first 6 months of life are high for a temperate-subarctic species, yet are clearly below the potential growth rate as shown in the laboratory (Shenker and Olla footnote 3). Similar but lower laboratory growth rates (1.2 mm/d) were observed for 100 to 150 mm juvenile red hake, *Urophycis chuss*, by Luczkovich and Olla (1983). Both of these species contrast markedly with larval juvenile growth in other taxa. Boehlert and Yoklavich (1983), for example, summarized laboratory and field growth measurements for 13 species in the genus *Sebastes* and noted growth rates ranging from 0.092 to 0.590 mm/d. Young sablefish thus utilize the neustonic and pelagic environment to rapidly reach sizes at which migration to the benthic adult habitat occurs.

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Literature Cited

BARKLEY, R. A.
1972. Selectivity of towed-net samplers. Fish. Bull., U.S. 70: 799-820.

BEAMISH, R. J., AND D. E. CHILTON.
1982. Preliminary evaluation of a method to determine the age of sablefish (*Anoplopoma fimbria*). Can. J. Fish. Aquat. Sci. 39:277-287.

BEAMISH, R. J., G. A. MCFARLANE, AND D. E. CHILTON.
1983. Use of oxytetracycline and other methods to validate a method of age determination for sablefish. *In* B. R. Meteff (editor), Proceedings of the International Sablefish Symposium, p. 95-116. Alaska Sea Grant College Program, Univ. Alaska, Fairbanks, Sea Grant Rep. 83-8.

BELL, F. H., AND J. T. GHARRETT.
1945. The Pacific coast blackcod, *Anoplopoma fimbria*. Copeia 1945:94-103.

BOEHLERT, G. W.
1982. Ontogenetic changes in growth and their relationship with temperature and habitat change. *In* G. M. Cailliet and C. A. Simenstad (editors), GUTSHOP '81. Fish food habits studies, p. 115-123. Proceedings of the Third Pacific Workshop, December 6-9, 1981, Pacific Grove, Calif.; Wash. Sea Grant Prog., Univ. Wash., Seattle, WSW-WO 82-2.

BOEHLERT, G. W., AND M. M. YOKLAVICH.
1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. Environ. Biol. Fishes 8:17-28.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

GEFFEN, A. J.
1982. Otolith ring deposition in relation to growth in herring (*Clupea harengus*) and turbot (*Scopthalmus maximus*) larvae.

Mar. Biol. (Berl.) 71:317-326.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

HEYAMOTO, H.
1962. Age of young sablefish, *Anoplopoma fimbria* (Pallas) 1811. J. Fish. Res. Board Can. 19:1175-1177.

LAROCHE, J. L., S. L. RICHARDSON, AND A. A. ROSENBERG.
1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull., U.S. 80:93-104.

LUCZKOVICH, J. J., AND B. L. OLLA.
1983. Feeding behavior, prey consumption, and growth of juvenile red hake. Trans. Am. Fish. Soc. 112:629-637.

MASON, J. C., R. J. BEAMISH, AND G. A. MCFARLANE.
1983. Sexual maturity, fecundity, spawning, and early life history of sablefish (*Anoplopoma fimbria*) off the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 40:2126-2134.

PHILLIPS, J. B.
1958. The fishery for sablefish, *Anoplopoma fimbria*. Calif. Fish Game 44:79-84.

PRUTER, A. T.
1954. Age and growth of the Oregon sablefish, *Anoplopoma fimbria*. Pac. Mar. Fish. Comm. Bull. 3:121-128.

SAMEOTO, D. D., AND L. O. JAROSZYNSKI.
1969. Otter surface sampler: a new neuston net. J. Fish. Res. Board Can. 26:2240-2244.

SHIROTA, A.
1970. Studies on the mouth size of fish larvae. Bull. Jpn. Soc. Sci. Fish. 36:353-368.

SAS INSTITUTE, INC.
1982. SAS users guide. SAS Institute, Inc., Raleigh, NC, 494 p.

TAUBERT, B. D., AND D. W. COBLE.
1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. J. Fish. Res. Board Can. 34:332-340.

THEILACKER, G. H.
1980. Changes in body measurement of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull., U.S. 78:685-692.

THOMPSON, W. F., JR.
1941. A note on the spawning of the blackcod (*Anoplopoma fimbria*). Copeia 1941:270.

WARE, D. M.
1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32:2503-2512.

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VERTICAL DISTRIBUTION OF ICHTHYOPLANKTON OFF THE OREGON COAST IN SPRING AND SUMMER MONTHS

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ABSTRACT

Day and night discrete-depth tows were taken off the Oregon coast in spring and summer months to assess the vertical distribution of ichthyoplankton in nearshore waters. Over 1,000 larvae representing 33 taxa of both coastal and offshore ichthyoplankton assemblages were taken; *Psettichthys melanostictus* was the most abundant coastal species and *Lyopsetta exilis* the most abundant offshore species. Larvae were generally most abundant at 10-30 m, near the seasonal thermocline in both day and night collections. Larval abundance in July was much higher than in April-May collections. Limited evidence for diel vertical migration suggests that *Psettichthys melanostictus* moves to surface waters at night and *Gadus macrocephalus* moves to deeper water at night. No trends of changes in depth distribution were observed with increasing size.

Knowledge of the vertical distributions of larval fishes is crucial to full understanding of their biology and to understanding the results of ichthyoplankton surveys (Ahlstrom 1959; Kendall and Naplin 1981). The interaction between vertical distributions and physical processes can have important effects on onshore-offshore distributions of planktonic organisms in upwelling regions such as the coastal northeastern Pacific (Peterson et al. 1979; Parrish et al. 1981; Wroblewski 1982; Rothlisberg et al. 1983). Near-surface distribution, for example, may result in shoreward transport in slicks associated with internal waves (Shanks 1983). In the coastal region off Oregon, the only information on larval fish vertical distribution is a comparison between abundances of *Parophrys vetulus* and *Isopsetta isolepis* larvae from neuston and oblique bongo net tows (Laroche and Richardson 1979) and one 24-h study with stratified samples taken by bongo nets without opening-closing devices (Richardson and Pearcy 1977). With the exceptions of the classic study by Ahlstrom (1959) and recent studies by Brewer et al. (1981) and Schlotterbeck and Connally (1982), little else is known about the vertical distribution of larval fishes in northeastern Pacific coastal waters. In this paper, we present information on vertical distributions of larval fishes off Oregon.

METHODS

Six series of samples were collected in 1982, four during daylight (30 April, 14 May, 2 and 13 July) and two during night (2 and 6-7 July). The first two series (30 April, 14 May) were taken at station NH10, 10 nmi (18.5 km) off Newport, OR, on the Newport hydroline (lat. 44°40′N; Fig. 1). All others were collected at NH5 (9.2 km offshore). Each sample series consisted of a variable number of tows at discrete depth strata from the surface to within about 4 m of the bottom (Table 1).

Tows were stepped oblique in five intervals of 3 min each, resulting in a total sampling time of 15 min in each 5 or 10 m depth stratum. The sampler was an opening-closing Tucker trawl (Clarke 1969) with three nets and a double-release mechanism operated by messengers. The nets were 0.505 mm mesh (Nitex[3]) with a 1 m^2 mouth; all tows were at a wire angle of 45° at approximate tow speeds from 0.9 to 1.1 m/s. At this angle, effective mouth area of the net is 0.71 m^2. An uncontaminated, discrete depth sample was collected in the second net by lowering the trawl with the first net open, opening the second net for the desired sampling time, and retrieving the trawl with the third net open. Water volumes filtered were estimated with General Oceanics flowmeters mounted in the center of each net. Volumes of water filtered usually ranged between 250 and 450 m^3/sample. Temperature and salinity data were collected throughout the water column on each cruise using Niskin bottles to collect

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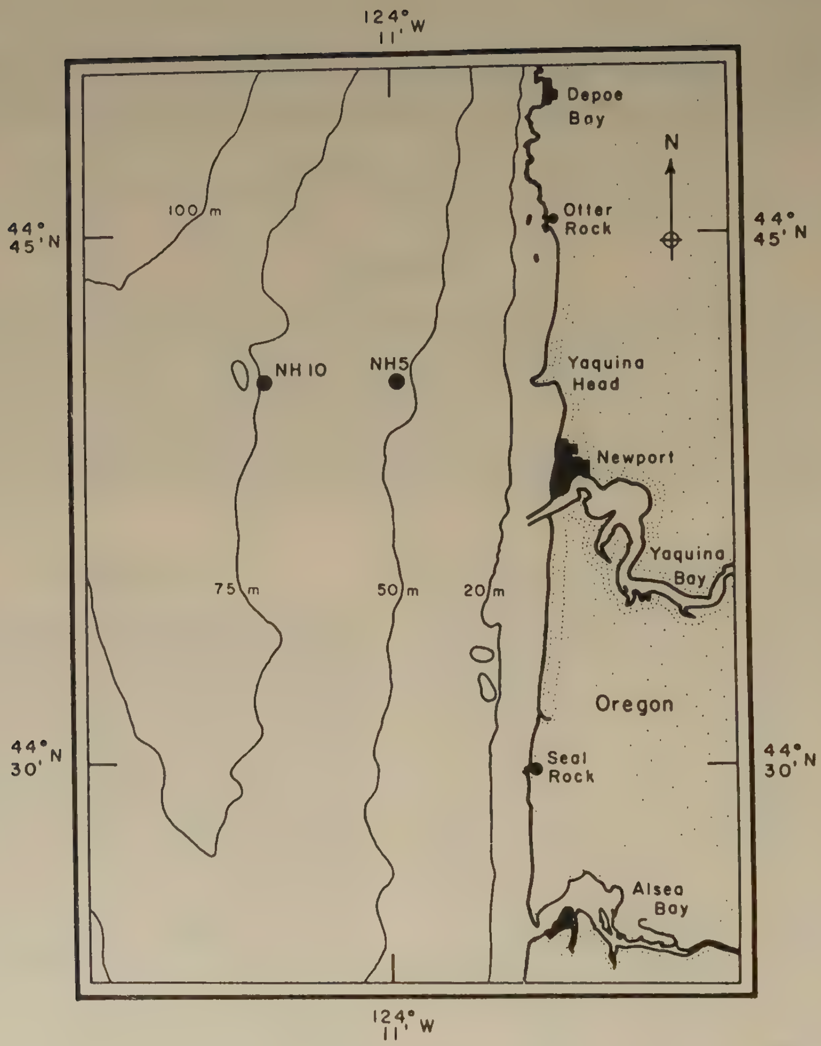
124° 11' W
44° 45' N
44° 45' N
44° 30' N
44° 30' N
124° 11' W
Depoe Bay
N
Otter Rock
100 m
NH 10
NH5
Yaquina Head
Newport
Yaquina Bay
75 m
50 m
20 m
Oregon
Seal Rock
Alsea Bay

FIGURE 1.—Locations of the sampling conducted during the present study. NH5 and NH10 indicate the stations used.

TABLE 1.—Number of tows per depth stratum with total volumes filtered. (Asterisk indicates that for subsequent analysis the NH10 day sample in the two deepest categories were combined with the 50-60 m stratum.) Sample times were as follows: Day—4/30, 1018-1547; 5/14, 0808-1600; 7/2, 0608-0907; 7/13, 0554-1048; night—7/2, 0016-0514, 7/6-7/7, 2330-0410.

	Day						Night		
	NH10		Total volume filtered (m^3)	NH5		Total volume filtered (m^3)	NH5		Total volume filtered (m^3)
Depth (m)	4/30	5/14		7/2	7/13		7/2	7/6-7/7	
0-5	2	2	1,682.7	2	2	1,392.6	2	2	1,574.8
5-10	2	2	1,783.7	2	2	1,451.2	2	2	1,575.7
10-20	2	2	1,595.7	1	2	862.9	2	2	1,292.9
20-30	2	2	1,796.7	1	2	929.3	2	2	1,237.6
30-40	1	2	1,415.8	1	2	920.5	1	2	1,184.0
40-50	1	2	1,488.1	1	2	920.9	1	2	1,034.8
50-60	1	2	1,891.2	1	2	671.3	1	1	808.3
60-70*	1	1	930.0	—	—	—	—	—	—
70-80*	—	1	704.8	—	—	—	—	—	—

water samples at 5 to 10 m intervals or using a self-contained Applied Microsystems CTD-12. The salinities of water bottle samples were determined in the laboratory using a Guideline 8400 autosalinometer. The CTD salinities from 13 July were not used because of suspected machine malfunction. The CTD temperatures from 13 July agreed with surface bucket temperatures and were used in our study.

Plankton samples were preserved at sea in 10% buffered Formalin. Samples were sorted for fish larvae in the laboratory using a dissecting microscope. Larvae were identified to the lowest possible taxon, measured (standard length), and stored in 5% buffered Formalin.

Larval abundances were calculated as number per 1,000 m^3 for each tow. The six sampling series were combined into three data sets, spring daytime samples (30 April and 14 May, NH10), summer daytime (2 and 13 July, NH5), and summer nighttime (2 and 6-7 July, NH5). In April and May the salinity profiles closely paralleled each other, with lower salinity at the surface, 30.5-31.0‰, than in deeper water, where salinities gradually increased to about 33-34‰ (Fig. 2a). Water temperatures above 50 m

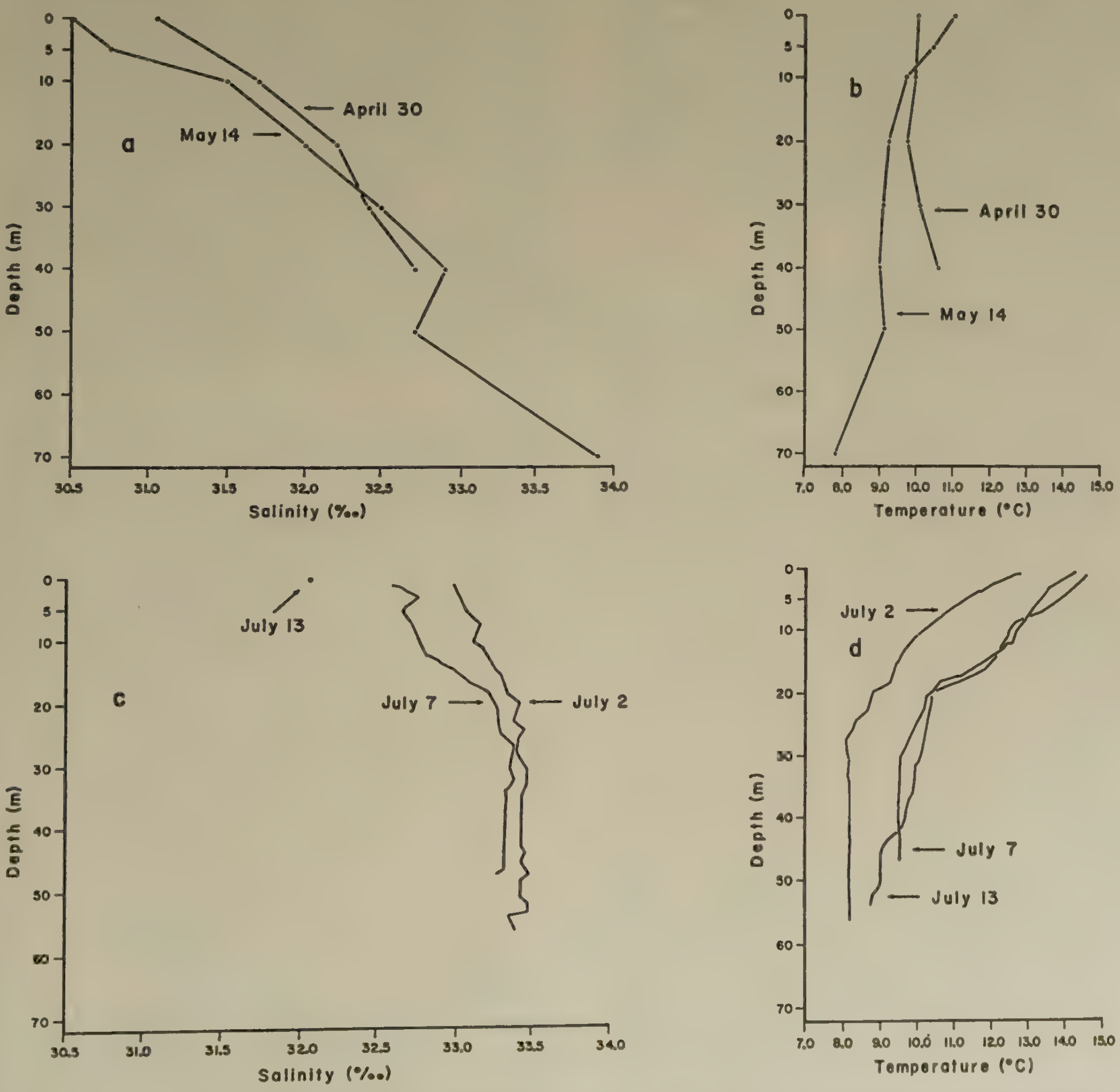

FIGURE 2.—Salinity and temperature profiles during the collections. a. Salinity profiles during the spring collections. b. Spring temperature profiles. c. Summer salinity profiles. d. Summer temperature profiles.

in April and May were about 9°-11°C (Fig. 2b). No thermocline was present. Thus, hydrographic regimes support grouping April and May samples together. Temperature and salinity profiles in April and May were typical for the winter Oregon hydrographic regime prior to the onset of late spring-early summer upwelling (Huyer 1977).

In July the salinity and temperature profiles differed from those in April and May (Figs. 2c, d). Salinities were more uniform in summer than spring throughout the water column, ranging from 32.0‰ at the surface to 33.4‰ below about 20 m (Fig. 2c). The temperature gradient in July was greater than in April and May due to warmer surface waters (Fig. 2d). Surface temperatures ranged from 12.8° to 14.6°C, decreasing with depth to about 8.2°-9.6°C at 40 m. A thermocline was present at about 10-20 m. Temperature and salinity profiles in July were typical of the summer Oregon hydrographic regime (Huyer 1977). Surface temperatures suggest that samples were not taken during active upwelling.

RESULTS

In this study, a total volume of 29,145.5 m^3 was filtered and 1,007 larvae, representing 33 taxa, were enumerated from 75 discrete depth tows. Larvae were most abundant in summer, with an abundance peak 10-30 m deep during daytime and 20-30 m deep during nighttime (Fig. 3). In spring, larvae were distributed relatively uniformly throughout the water column below 5 m with small abundance peaks at 10-20 and 40-50 m. During daytime in both spring and summer, larvae were least abundant at the surface (0-5 m), although abundance at the surface increased at night. The depth distribution at night also differed in having a secondary abundance peak near the bottom (50-60 m) and greater overall larval abundance than during the day.

The larval fish species were categorized as coastal (most abundance 2-28 km from the coast, see Tables 2, 3, and 4), or offshore (most abundant 37-111 km from the coast, see Tables 5, 6, and 7), according to larval assemblages described by Richardson and Pearcy (1977). Most larvae in this study were of the coastal assemblage because samples were collected at NH5 and NH10 (9.2 and 18.5 km from the coast, respectively). The spawning seasons of the dominant species off Oregon are discussed in Mundy (1984); most of the fall-winter spawning species were not represented in this study. Since many species were not abundant enough to demonstrate trends, only the dominant species will be discussed below.

Coastal Assemblage

Gadus macrocephalus, *Microgadus proximus*, *Isopsetta isolepis*, and *Psettichthys melanostictus* larvae were abundant in all three sampling periods (Tables 2, 3, 4, Fig. 4). *Gadus macrocephalus* larvae were most abundant during the day at 20-30 m in both spring and summer, but were very abundant in the deepest stratum (below 50 m) in night samples (Fig. 4). *Microgadus proximus* larvae do not show as clear a trend, but were most abundant in deeper water during summer, particularly at nighttime. In spring they were distributed throughout the water column. *Isopsetta isolepis* and *P. melanostictus* were also most abundant in nighttime samples. More *I. isolepis* larvae were found at 10-20 m in spring, whereas in summer they were collected throughout the water column, with abundance peaks near the bottom. *Psettichthys melanostictus* larvae were more abundant in summer than spring samples. During daytime in summer, *P. melanostictus* were most abundant below 10 m, whereas at nighttime, although found throughtout the water column, they were most abundant in waters shallower than 10 m (Fig. 4).

Seasonal abundance changes were observed for

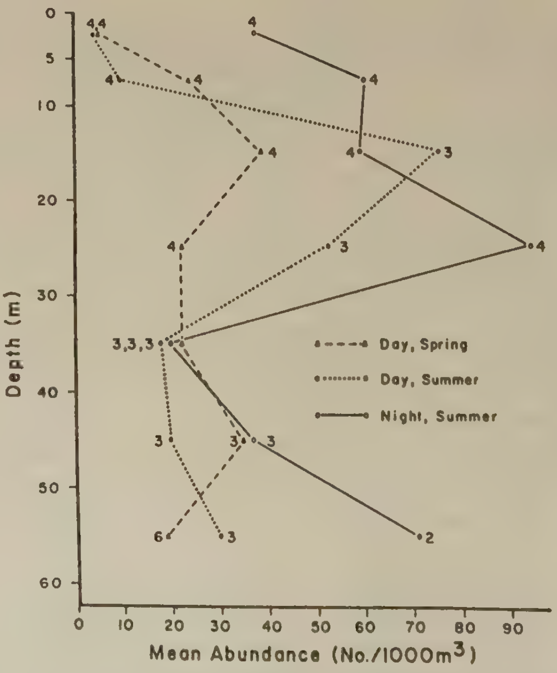

FIGURE 3.—Overall larval abundance (larvae per 1,000 m^3) for all collections. Numbers adjacent to data points indicate the number of samples taken.

TABLE 2.—Mean abundances (number per 1,000 m^3) for coastal larval species from spring (day only) samples.

Species	Depth (m)							
	0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Clupeidae								
Clupea harengus	—	—	1.76	2.36	1.25	0.75	—	0.87
Osmeridae								
Undetermined spp.	—	1.85	5.02	1.22	1.51	1.16	0.23	1.57
Gadidae								
Gadus macrocephalus	1.14	0.53	5.69	7.59	2.91	—	0.89	2.68
Microgadus proximus	1.13	2.04	3.87	2.97	0.73	2.95	0.45	2.02
Cottidae								
Artedius fenestralis	—	—	—	—	—	—	—	—
Artedius harringtoni	—	—	—	—	—	0.75	0.41	0.17
Artedius meanyi	—	—	—	—	—	—	0.44	0.06
Clinocottus embryum	—	—	—	—	—	—	—	—
Cottus asper	—	0.53	—	—	—	—	—	0.08
Radulinus asprellus	—	—	—	—	—	—	2.60	0.37
Agonidae								
Odontopyxis trispinosa	—	—	—	—	—	—	0.23	0.03
Cyclopteridae spp. 1	—	—	—	0.74	2.29	3.64	0.45	1.02
Undetermined spp.	—	—	—	0.47	—	—	—	0.07
Bathymasteridae								
Ronquilus jordani	—	0.59	—	—	—	—	—	0.08
Ptilichthyidae								
Ptilichthys goodei	—	—	0.94	—	—	—	—	0.13
Bothidae								
Citharichthys stigmaeus	—	—	—	—	0.73	—	0.87	0.23
Pleuronectidae								
Isopsetta isolepis	0.49	1.79	7.78	2.86	—	1.29	0.66	2.12
Lepidopsetta bilineata	—	0.59	0.94	—	—	—	—	0.22
Parophrys vetulus	—	0.59	1.76	—	—	—	0.45	0.40
Psettichthys melanostictus	1.48	5.46	5.58	—	0.73	—	0.44	1.96

TABLE 3.—Mean abundances (number per 1,000 m^3) for coastal larval species from summer day samples.

Species	Depth (m)							
	0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Clupeidae								
Clupea harengus	—	—	—	—	—	—	—	—
Osmeridae								
Undetermined spp.	—	—	—	—	—	—	3.69	0.53
Gadidae								
Gadus macrocephalus	—	—	1.38	12.01	1.08	1.09	—	2.22
Microgadus proximus	—	—	2.01	1.01	—	3.28	3.49	1.40
Cottidae								
Artedius fenestralis	—	—	1.00	1.15	—	—	—	0.31
Artedius harringtoni	—	0.68	4.54	3.30	2.18	2.19	3.39	2.33
Artedius meanyi	—	—	3.38	2.02	1.10	—	—	0.93
Clinocottus embryum	—	—	—	—	—	—	—	—
Cottus asper	—	0.53	—	—	—	—	—	0.08
Radulinus asprellus	—	—	—	—	—	—	—	—
Agonidae								
Odontopyxis trispinosa	—	—	—	1.01	—	—	—	0.14
Cyclopteridae spp. 1	—	—	—	2.22	2.16	—	—	0.63
Undetermined spp.	—	—	2.16	4.18	1.08	2.18	6.05	2.24
Bathymasteridae								
Ronquilus jordani	0.63	0.70	2.01	1.01	—	—	—	0.62
Ptilichthyidae								
Ptilichthys goodei	—	—	—	—	—	—	—	—
Bothidae								
Citharichthys stigmaeus	—	—	1.00	—	—	—	—	0.14
Pleuronectidae								
Isopsetta isolepis	—	—	2.07	1.01	2.20	—	4.82	1.44
Lepidopsetta bilineata	—	—	—	—	—	—	—	—
Parophrys vetulus	—	—	—	—	—	—	—	—
Psettichthys melanostictus	0.98	2.03	22.98	7.48	3.24	3.26	11.18	7.31

TABLE 4.—Mean abundances (number per 1,000 m^3) for coastal larval species from summer night samples.

Species	Depth (m)							Mean
	0-5	5-10	10-20	20-30	30-40	40-50	>50	
Clupeidae								
Clupea harengus	—	—	—	—	—	—	—	—
Osmeridae								
Undetermined spp.	—	4.42	15.15	4.56	—	0.75	1.12	3.71
Gadidae								
Gadus macrocephalus	—	—	—	0.82	3.16	8.11	22.98	5.01
Microgadus proximus	0.66	0.61	—	4.66	1.95	3.29	6.91	2.58
Cottidae								
Artedius fenestralis	3.20	—	0.78	1.57	—	0.75	2.60	1.27
Artedius harringtoni	1.35	4.41	5.44	11.30	0.73	1.27	1.40	3.70
Artedius meanyi	0.66	4.48	0.71	4.12	0.74	1.01	3.62	2.19
Clinocottus embryum	0.66	—	—	—	—	—	—	0.09
Cottus asper	—	—	—	—	—	—	—	—
Radulinus asprellus	—	—	—	—	—	—	—	—
Agonidae								
Odontopyxis trispinosa	—	—	—	—	—	—	2.50	0.36
Cyclopteridae spp. 1	—	—	0.77	0.79	—	—	—	0.22
Undetermined spp.	—	—	—	3.96	0.73	—	4.74	1.35
Bathymasteridae								
Ronquilus jordani	—	—	0.71	1.70	—	1.27	—	0.53
Ptilichthyidae								
Ptilichthys goodei	—	—	—	—	—	—	—	—
Bothidae								
Citharichthys stigmaeus	—	—	—	0.74	0.74	—	—	0.21
Pleuronectidae								
Isopsetta isolepis	—	2.57	1.63	6.50	2.64	10.90	1.12	3.62
Lepidopsetta bilineata	—	—	—	—	—	—	—	—
Parophrys vetulus	0.66	—	0.71	—	—	—	—	0.20
Psettichthys melanostictus	24.63	31.37	13.65	18.86	7.78	6.07	6.91	15.61

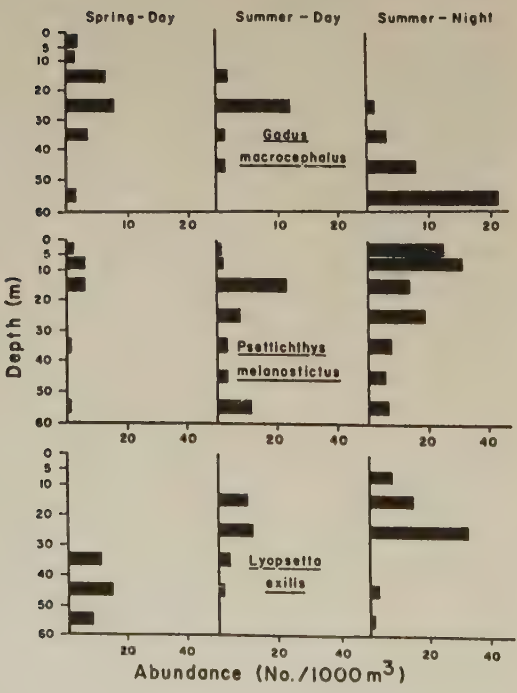

FIGURE 4.—Vertical abundance patterns of the three most abundant taxa (*Gadus macrocephalus*, *Psettichthys melanostictus*, and *Lyopsetta exilis*) during the three sampling periods.

Artedius and cyclopterid species. *Artedius fenestralis*, *A. harringtoni*, and *A. meanyi* were taken almost exclusively in the summer sampling period. All species were most abundant in nighttime samples. During the day, *A. harringtoni* larvae were distributed relatively uniformly throughout the water column from about 10 to 60 m, whereas at night most larvae were taken from the 5-30 m depth strata. Most cyclopterid larvae collected in spring were the larval type referred to as Cyclopteridae spp. 1 by Richardson and Pearcy (1977). Other cyclopterid species were more abundant in summer. Most cyclopterid larvae were collected below 20 m during both night and day, and in summer were abundant at the deepest sampling depths.

Osmerid larvae of undetermined species had a unique distribution pattern. They were abundant during spring, rare during summer daytime samples, and most abundant during summer nighttime samples. During both spring and summer, larvae were most abundant at the 10-20 m depth stratum.

Offshore Assemblage

Spring to summer differences in abundance patterns were more distinct for offshore larval species as compared with coastal species (Tables 5, 6, 7).

TABLE 5.—Mean abundances (number per 1,000 m^3) for offshore larval species from spring (day only) samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Offshore								
Engraulidae								
Engraulis mordax	—	—	—	—	—	—	—	—
Bathylagidae								
Bathylagus ochotensis	—	—	0.56	—	0.78	7.28	0.87	1.36
Bathylagus pacificus	—	—	—	—	—	—	0.22	0.03
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	0.75	—	0.11
Protomyctophum thompsoni	—	—	—	—	—	1.74	1.19	0.42
Stenobrachius leucopsarus	0.49	6.79	2.76	0.47	—	—	—	1.50
Bythitidae								
Brosmophycis marginata	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes spp.	—	2.73	1.06	1.49	—	—	—	0.75
Bothidae								
Citharichthys sordidus	—	—	—	—	—	—	—	—
Pleuronectidae								
Glyptocephalus zachirus	—	—	1.06	—	—	—	—	0.15
Lyopsetta exilis	—	—	—	—	11.27	14.9	8.56	4.96
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	—	1.49	—	—	—	0.21

TABLE 6.—Mean abundances (number per 1,000 m^3) for offshore larval species from summer day samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Offshore								
Engraulidae								
Engraulis mordax	0.98	2.13	—	—	—	—	—	0.44
Bathylagidae								
Bathylagus ochotensis	—	—	—	—	—	—	—	—
Bathylagus pacificus	—	—	—	—	—	—	—	—
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	—	—	—
Protomyctophum thompsoni	—	—	—	—	—	—	—	—
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—
Bythitidae								
Brosmophycis marginata	1.49	0.73	—	—	—	—	—	0.32
Scorpaenidae								
Sebastes spp.	—	0.65	3.03	1.08	1.10	—	—	0.84
Bothidae								
Citharichthys sordidus	—	0.73	—	—	—	—	—	0.10
Pleuronectidae								
Glyptocephalus zachirus	—	2.11	19.55	4.52	—	—	—	3.74
Lyopsetta exilis	—	—	10.03	11.53	4.38	2.13	—	4.01
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	—	—	—	1.10	—	0.16

Only *Sebastes* and *Lyopsetta exilis* larvae were abundant in all three sampling periods. *Sebastes* larvae were most abundant in nighttime samples, when they were mainly collected in shallow water (0-20 m). In both spring and summer daytime samples they were also in relatively shallow waters (5-40 m), although they were not abundant at the shallowest stratum (0-5 m). During day, *L. exilis* larvae were distributed in deeper water, particularly in spring, when all larvae were collected below 30 m (Fig. 3). At night, most *L. exilis* were shallower, between 5 and 30 m.

Two species, *Bathylagus ochotensis* and *Stenobrachius leucopsarus*, were collected only in spring samples. These two species were predominantly collected at different depths with *B. ochotensis* found

TABLE 7.—Mean abundances (number per 1,000 m^3) for offshore larval species from summer night samples.

Species	Depth (m)							Mean
	0-5	5-10	10-20	20-30	30-40	40-50	>50	
Offshore								
Engraulidae								
Engraulis mordax	4.09	3.76	—	—	—	—	—	1.12
Bathylagidae								
Bathylagus ochotensis	—	—	—	—	—	—	—	—
Bathylagus pacificus	—	—	—	—	—	—	—	—
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	—	—	—
Protomyctophum thompsoni	—	—	—	—	—	—	—	—
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—
Bythitidae								
Brosmophycis marginata	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes spp.	3.86	0.68	2.38	0.82	—	—	1.12	1.27
Bothidae								
Citharichthys sordidus	—	—	0.78	—	0.74	1.27	10.27	1.87
Pleuronectidae								
Glyptocephalus zachirus	0.66	0.68	0.77	0.91	—	—	—	0.43
Lyopsetta exilis	—	8.28	15.05	32.99	—	3.53	1.12	8.71
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	0.71	—	—	—	1.12	0.26

in deeper water (40-50 m) and *S. leucopsarus* in shallow water (5-20 m).

Two species of larval flatfishes and *Engraulis mordax* were collected only in summer samples. *Glyptocephalus zachirus* were most abundant during day at 5-30 m, and *Citharichthys sordidus* at night below 50 m. *Engraulis mordax* larvae were collected only above 10 m. *Engraulis mordax* were most abundant at night when more than half were in very shallow waters, <5 m. During the day, more *E. mordax* were found at 5-10 m than at 0-5 m.

A relationship between larval size and depth was not evident for any species. Because of the low abundances of larvae, however, this relationship could not be adequately considered for most species. A change in larval size with season was demonstrated for the most abundant species (Table 8), with mean larval standard lengths of all species greater in summer than in spring samples. There were no obvious differences between the size of larvae caught in day and night summer samples.

DISCUSSION

Peak abundances of all taxa combined occurred at 10-30 m on all sample dates (Fig. 3) and characterized several individual taxa during the day, including *Clupea harengus*, Osmeridae, *Gadus macrocephalus*, *Sebastes* spp., and *Parophrys vetulus*, as well as *Lyopsetta exilis* and *Psettichthys melanostictus* in the summer. The 10-30 m depth range bracketed the lower boundary of the seasonal thermocline in July, although no thermocline was present in April-May (Fig. 2). This trend for the peak abundance of fish larvae to be centered near the thermocline is similar to that found in other regions (Ahlstrom 1959; Miller et al. 1963; Kendall and Naplin 1981).

The trend for most larvae to be found in midwater was similar to that described by Brewer et al. (1981) for their deepest stations off southern California. We did not find large concentrations of larvae near the bottom as they did, except at night, when gadids, cottids, cyclopterids, and pleuronectids were abundant. Our sampling gear was ineffective just above the bottom as compared with the roller-equipped gear used by Brewer et al. (1981).

Richardson and Pearcy (1977) found larvae to be most abundant at 0-10 m and least abundant at 51-100 m during late May off Oregon. We found larvae to be most abundant at 10-30 m. This difference may be due to differences in hydrography and station locations. Their station was 18 km offshore, closer to the shelf break where the depth of water was over 150 m deep. The faunal composition in each study was also different. Richardson and Pearcy (1977) captured more specimens of several surface-associated taxa than we did, including large *Clupea harengus*, *Stenobrachius leucopsarus*, *Ronquilus jordani*, and *Ammodytes hexapterus*. We captured higher densities of deeper dwelling taxa, including gadids and cottids. Several taxa taken in both studies had different distributions in each, including *Sebastes*

TABLE 8.—Ranges and mean standard lengths (mm) for dominant fish larvae. *N* = number of larvae; Min. = minimum; Max. = maximum.

Species	Spring: Day				Summer: Day				Summer: Night			
	N	Min.	Mean	Max.	*N*	Min.	Mean	Max.	*N*	Min.	Mean	Max.
Coastal												
Clupea harengus	10	7	8.2	9	0	—	—	—	0	—	—	—
Osmerid	17	3	7.1	17	3	29	33.1	38	35	23	31.8	40
Gadus macrocephalus	29	8	10.8	20	17	9	13.6	17	28	9	13.3	19
Microgadus proximus	22	6	10.9	19	9	11	21.3	36	18	6	18.4	33
Artedius fenestralis	0	—	—	—	2	11	12.0	13	8	10	11.6	13
Artedius harringtoni	2	6	6.5	7	15	5	8.2	13	33	5	8.6	14
Artedius meanyi	1	—	4.9	—	6	7	9.9	16	19	7	9.4	18
Radulinus asprellus	10	6	7.6	9	0	—	—	—	0	—	—	—
Liparid type 1	12	4	5.7	6	4	3	3.1	3	2	3	3.5	4
Liparid unknown	1	—	10.2	—	14	5	16.7	25	10	15	20.4	23
Ronquilus jordani	1	—	6.6	—	5	22	27.1	33	5	24	24.1	25
Isopsetta isolepis	22	4	8.9	21	9	10	20.0	23	28	7	16.1	23
Psettichthys melanostictus	—	3	7.0	22	41	9	20.0	27	150	8	20.8	28
Offshore												
Engraulis mordax	0	—	—	—	4	12	13.5	15	12	7	13.1	16
Bathylagus ochotensis	16	5	8.1	19	0	—	—	—	0	—	—	—
Stenobrachius leucopsarus	19	3	5.2	9	0	—	—	—	0	—	—	—
Sebastes spp.	8	4	4.7	6	6	4	14.6	18	12	12	16.0	18
Citharichthys sordidus	0	—	—	—	1	—	20.5	—	11	17	37.8	40
Glyptocephalus zachirus	2	13	25	37	22	14	29.9	39	4	22	34.5	50
Lyopsetta exilis	71	4	8.4	15	27	11	13.2	16	79	7	12.2	20

spp., Cyclopteridae spp. 1, and *Isopsetta isolepis*. These differences indicate the need for more extensive sampling before the variability of vertical distributions off Oregon can be understood, particularly as they relate to hydrographic conditions.

We found *Engraulis mordax* larvae entirely at 0-10 m. Brewer et al. (1981) found greater concentrations of *Engraulis* below 10 m, while Ahlstrom (1959) found *Engraulis* to be concentrated in the upper 23 m with some specimens occurring to 105 m. Off Oregon, *Engraulis* larvae are found concentrated at 0-20 m (Richardson 1973), in association with the Columbia River plume, a lens of warm, low salinity water usually 20-40 m deep (Richardson 1980). Our limited data suggest that *Engraulis mordax* larvae occur at depths that would place them within the plume, rather than beneath it or at its boundary. The vertical distribution suggests restriction to the warmest part of the water column (Fig. 2d); northern anchovies rarely spawn in waters with surface temperatures below 14°C (Lasker et al. 1981).

The seasonal differences in species composition between the April-May and July samples were those that would be expected in samples from winter and summer hydrographic regimes, except that *Artedius fenestralis* and *A. meanyi* have been taken in April and May of other years (Mundy 1984). The presence of *Clupea harengus*, *Radulinus asprellus*, myctophid, and bathylagid larvae only in April-May, during a winter hydrographic regime, is expected from previous studies (Richardson and Pearcy 1977; Mundy 1984).

Studies of day/night differences in the distribution of fish larvae are confounded by daytime avoidance of nets by larvae (Ahlstrom 1959). Daytime avoidance of nets is suggested in our study by the greater numbers of larvae taken during the night than day at all but two depth strata. The lack of length differences between larvae caught in day and night, however, and the fact that no taxa were taken only in night samples during July suggests that diurnal net avoidance was not related to taxon or size. The same comparisons with 70 cm bongo net samples (Richardson and Pearcy 1977) suggest that diurnal avoidance by large larvae was greater for bongo nets than for the Tucker trawl.

Evidence for vertical migration exists for several species in this study (Tables 3, 4, 6, 7). *Psettichthys melanostictus* abundance in surface waters (0-10 m) increased greatly at night (Fig. 4). *Engraulis mordax* were most abundant at 5-10 m than 0-5 m during the day, but more evenly distributed at night. This could be due either to vertical migration or net avoidance in the shallowest stratum during the day. Ahlstrom (1959), however, presented evidence for negative phototaxis by anchovy larvae, and Hunter and Sanchez (1976) demonstrated nighttime migration to the surface in larvae larger than 10 mm SL. Thus larvae migrate upwards at night, but are constrained to shallower water in the day as compared with the southern subpopulation.

The clearest case of vertical migration was that of *Gadus macrocephalus* (Tables 3, 4), which was most abundant at 20-30 m in the day and deeper than 50 m at night. The migration of this species was primarily responsible for the increased total abundance of larvae near the bottom at night (Fig. 3). This pattern of movement is similar to that observed for larval *Ammodytes personatus* by Yamashita et al. (1985), who suggested that this reverse vertical migration allowed feeding in daytime and avoidance of migrating predators at night. This nocturnal descent, not previously reported for *Gadus* larvae, should be confirmed with further sampling. *Gadus morhua* larvae 3.8-4.9 mm long move from deeper water in the day to 0-2 m at night, and descend in the water column with growth (Hardy 1978). Larvae of another gadid, *Melanogrammus aeglefinus*, are most common in the thermocline and their depth of greatest abundance fluctuates as the thermocline depth changes with rotary tidal currents, causing occasional descent in the water column at night (Miller et al. 1963).

Offshore taxa in Oregon coastal waters should occur in greatest numbers during onshore surface water transport during winter and early spring. This was true in our study for the mesopelagic Myctophidae and Bathylagidae, but not for other offshore assemblage taxa (Tables 5, 6, 7). Almost all of the bathylagid and myctophid larvae except *Stenobrachius leucopsarus* were found below 30 m. Ahlstrom's (1959) work confirms these general distributions; he found most larvae of the genera taken in this study (*Electrona* = *Protomyctophum*; *Lampanyctus* = *Stenobrachius*) at depths >56 m, beneath the thermocline, except *Stenobrachius*. He found *Stenobrachius* to have the shallowest distribution of all myctophid larvae in his study (0-41 m). Richardson and Pearcy (1977) also found *Stenobrachius* larvae to be in shallow waters (0-50 m) with many at 0-10 m during the day. The distribution of larval mesopelagic fishes, or other offshore taxa, cannot be related to the depth of onshore transport because virtually nothing is known about the depth of winter onshore transport off Oregon (Peterson et al. 1979; Huyer[4]). Both deep and surface dwelling larvae of mesopelagic fishes collected in our study appear to be transported onshore, however, suggesting that transport occurs over a broad depth range off Oregon.

ACKNOWLEDGMENTS

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

BREWER, G. D., R. J. LAVENBERG, AND G. E. MCGOWAN.
1981. Abundance and vertical distribution of fish eggs and larvae in the southern California bight: June and October 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:165-167.

CLARKE, M. R.
1969. A new midwater trawl for sampling discrete depth horizons. J. Mar. Biol. Assoc. U.K. 49:945-960.

HARDY, J. D., JR.
1978. Family Gadidae: *Gadus morhua* Linnaeus, Atlantic cod. *In* Development of fishes of the Mid-Atlantic Bight, an atlas of egg, larval + juvenile stages. Vol. II, p. 236-259. U.S. Dep. Inter., Fish Wildl. Serv.

HUNTER, J. R., AND C. SANCHEZ.
1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:847-855.

HUYER, A.
1977. Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. Limnol. Oceanogr. 22:442-453.

KENDALL, A. W., JR., AND N. A. NAPLIN.
1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. Fish. Bull., U.S. 79:705-726.

LAROCHE, J. L., AND S. L. RICHARDSON.
1979. Winter-spring abundance of larval English sole, *Parophrys vetulus*, between the Columbia River and Cape Blanco, Oregon during 1972-1975 with notes on occurrences of three other pleuronectids. Estuarine Coastal Mar. Sci. 8:455-476.

LASKER, R., J. PELÁEZ, AND R. M. LAURS.
1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy *Engraulis mordax*. Remote Sens. Environ. 11:439-453.

MILLER, D., J. B. COLTON, JR., AND R. R. MARAK.
1963. A study of the vertical distribution of larval haddock. J. Cons. Perm. Int. Explor. Mer 28:37-49.

MUNDY, B. C.
1984. Yearly variation in the abundance and distribution of fish larvae in the coastal upwelling zone off Yaquina Head, Oregon from June 1969 to August 1972. MS Thesis, Oregon State Univ., Corvallis, 158 p.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1:175-203.

PETERSON, W. T., C. B. MILLER, AND A. HUTCHINSON.
1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Res. 26A:467-494.

---

[4] A. Huyer, Associate Professor, Oregon State University, Corvallis, OR 97331, pers. commun. 29 September 1983.

RICHARDSON, S. L.

1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71: 697-711.

1980. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855-876.

RICHARDSON, S. L., AND W. G. PEARCY.

1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

ROTHLISBERG, P. C., J. A. CHURCH, AND A. M. G. FORBES.

1983. Modelling the advection of vertically migrating shrimp larvae. J. Mar. Res. 41:511-538.

SCHLOTTERBECK, R. E., AND D. W. CONNALLY.

1982. Vertical stratification of three nearshore southern California larval fishes *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*. Fish. Bull., U.S. 80:895-902.

SHANKS, A. L.

1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311-315.

WROBLEWSKI, J. S.

1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. Deep-Sea Res. 29A:665-686.

YAMASHITA, Y., D. KITAGAWA, AND T. AOYAMA.

1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel, *Ammodytes personatus*. Bull. Jpn. Soc. Sci. Fish. 51:1-5.

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Subsurface Temperature Variability Along the West Coast of North and South America

The anomaly of temperature at 100 m along the coast of North and South America was computed from subsurface temperature profiles from the "Master Oceanographic Observation Data Set" (MOODS) at Fleet Numerical Oceanography Center in Monterey, California. These files include all available bottle casts, MBT, XBT, and CTD profiles, and real-time radio reports of subsurface temperature. For 1951-84, the anomaly of temperature at 100 m was computed each month relative to the long-term mean for that period. Data for all years before 1951 were combined into a single composite year, labeled 1951. The computations were made for 27 areas, each spanning 3 degrees of latitude from British Columbia to Chile (50°N to 30°S, Figure 1). The zonal extent of each area was chosen so that each area would extend roughly the same distance offshore, and varied from 4 degrees of longitude in regions having a meridional coast to a maximum of 10 degrees of longitude off southern Mexico and Guatemala where the coastline is nearly zonal. There were a total of 115,515 temperature profiles available for the 27 areas, with almost 85% from north of 15°N. Observations are sparse for the areas off southern Peru, Chile, and Central America, particularly in the early 1950's and also in recent years due to delays in data assembly. The computed anomalies were smoothed to remove small variations in time and space by first passing the array through a nonlinear median filter in which the central value of each 3 x 3 subarray was replaced by the median of the 9 values in the subarray. This was followed by a triple pass through a linear smoother for subarrays of 3 months by 5 areas. The subarrays were extended farther in space than in time to emphasize the strong coastwise coherence of the data. In this smoothing, the central value of each 3 x 5 subarray was replaced by one-half of the original value plus one-half of the mean of the 14 surrounding values

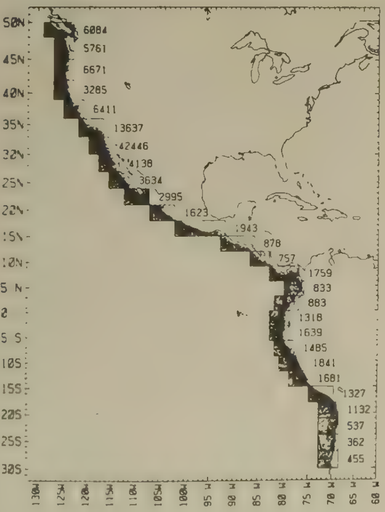

FIGURE 1 (*Brainard and McLain*) *Locations of 27 areas along the eastern Pacific from 50°N to 30°S and the distribution of observations of temperature at 100 m within the areas. The number of observations is printed to the right of each area. Note the scarcity of observations off Chile, southern Peru, and Central America.*

A time-latitude contour plot of the smoothed anomaly field (Figure 2) shows each of the major anomalous warm and cold events of the past three decades. Each of the well-documented El Niño events—1957-58, 1965, 1969, 1972-73, 1976-77, and 1982-83 (Quinn *et al.*, 1978)—are clearly evident and show strong coherence along the coast. The extreme spatial extent and magnitude of the 1982-83 event distinguish it as the most significant warm event of the period. It was the only event having an anomaly greater than 1°C north of Pt. Conception. Norton *et al.* (1984) attribute the extreme character of the 1982-83 event in the California Current system to the synchronous occurrence of warming processes associated with equatorial warming and midlatitude atmospheric perturbations. The 1954-56 cold event is comparable in extent and duration with the 1982-83 warm event. Only these two events retain their anomalous character for the entire distance from British Columbia to Chile. Following the 1954-56 cold event, the monthly mean temperature of coastal waters from the equator to Baja California rose from 1°-2°C below the mean (1956) to 1°-3°C above the mean (1957) in 5-10 months. This represents the highest rate of temperature change during the 33 year period and was associated with changes in atmospheric circulation (Huang, 1972).

The leading edges of the warm anomalies tend to lag in time with distance poleward from the equator, suggesting poleward propagation of anomalies. (Insufficient data are available to track the leading edge of the 1954-56 cold event.) The approximate speeds of propagation along the coast for the 1957-58, 1972-73, 1976-77, and 1982-83 warm events are summarized as follows:

Dates	**Initial latitude**	**Final latitude**	**Approximate speed of propagation** (km/day)
Oct '56-Jun '57	14°S	22°N	23
Feb '72-Jan '73	1°S	25°S	9
-Aug '72	1°S	30°N	26
May '76-May '77	4°S	19°S	6
-Sep '76	4°S	34°N	56
Apr '82-Apr '83	1°S	22°S	7
-Jul '82	1°S	28°N	45
-Nov '82	1°S	46°N	32

In contrast with the general poleward propagation, the 1957-58 warm event appeared to originate off southern Peru (about 14°S) and propagate north across the equator to Baja California. Each of the other three events originated near the equator and propagated poleward. In the four cases, the propagation to the north was several times faster than the propagation to the south. All of the propagation speeds were slower than the theoretical speeds of coastal Kelvin waves or coastally trapped waves, suggesting changes in advection as well as the passage of propagating waves.

The data suggest the existence of a long-term warming trend of the coastal waters, particularly off western North America. Extreme cold conditions occurred in the early 1950's, followed by warming in 1957-58, moderate conditions from 1960 to 1975, warm conditions since 1976, and extreme warm conditions in 1982-83. Such a trend can also be seen in sea-level observations, which are related to the vertical integral of the density structure and thus temperature, dating to the 1920's (McLain *et al.*, in press). Plots of anomaly of temperature at the surface and at 200 m reveal the same characteristics as at 100 m, but generally with lower magnitudes. The warming trend thus represents a general deepening of the thermal structure along the coast. Such a deepening would cause a change in the slope of the thermal structure normal to the coast and a tendency to increase transport of warm water and associated organisms poleward along the coast. Also, deepening the thermal structure would reduce the biological productivity of the surface waters by reducing the ability of upwelling-favorable winds to upwell deeper than normal nutrient-rich water (McLain *et al* ., in press).

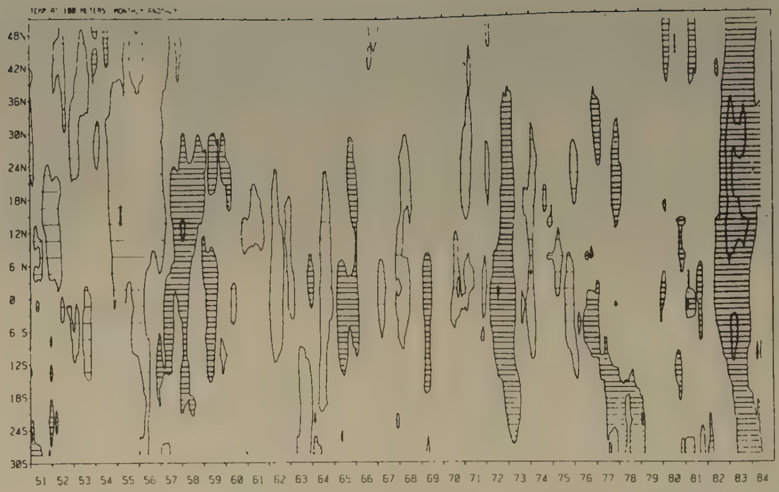

FIGURE 2 (*Brainard and McLain*)

Time-latitude contour plot of anomaly of temperature at 100 m along the coast from 50°N to 30°S for 1951 to 1984. Positive anomalies >0.5°C are indicated by cross-hatching (overlapping plus signs) and negative anomalies < −0.5°C by widely spaced horizontal lines (overlapping minus signs). The heavier contour lines represent positive anomalies >1.5°C and <2.5°C. Blank areas on the plot represent anomalies between +0.5°C and −0.5°C or nonavailability of data.

References

Huang, J. C. K. (1972) Recent decadal variation in the California Current system. *Journal of Physical Oceanography*, *2*, 382-390.

McLain, D. R., R. E. Brainard, and J. Norton (1984) Anomalous warm events in eastern boundary current systems. In: *Symposium on Comparative Studies*. CalCOFI Conference, Idyllwild, CA.

Norton, J., D. R. McLain, R. E. Brainard, and D. Husby (1984) The 1982-83 El Niño event off Baja and Alta California and its ocean climate context. *Proceedings of Meeting on Niño Effects in the Eastern Subarctic Pacific*. W. Wooster and D. Fluharty, editors.

Quinn, W. H., D. O. Zopf, K. S. Short, and R. T. W. K. Yang (1978) Historical trends and statistics of the Southern Oscillation, El Niño, and Indonesian droughts. *Fishery Bulletin*, *76*, 663-678.

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Exploitation of California Sea Lions, *Zalophus californianus*, Prior to 1972

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Introduction

This article summarizes the results of an investigation made into historical sealing activities on the California coast and Channel Islands. Of primary interest were the numbers of California sea lions, *Zalophus californianus*, killed on San Miguel Island. The harvesting of the northern or Steller sea lion, *Eumetopias jubatus*, is also discussed. Literature was reviewed for records on the number of sea lions taken for commercial purposes. Many other potential sources of information on numbers of animals killed were also investigated. A summary of take levels is given in Table 1.

Table 1.—Summary of sea lion (*Eumetopias* and *Zalophus*) kill, 1800-1972.

Year	Species indicated	Population level	Harvest	Source
1800-1850	Mixed	Pristine	30-70 animals/year	Ogden, 1933
1860-1870[1]	Mixed	High	9,000-15,000	Scammon, 1874
1874[1]	Mixed	Low	9,000-15,000	Bartholomew, 1967
1899	*Eumetopias*	Moderate	2,000 on Ano Nuevo Island	Bonnot, 1928b
1900	*Eumetopias*	Moderate	"Great many"	Rutter et al., 1902
1907	*Zalophus*	Low	Practically all bulls killed on San Miguel Island	Bonnot, 1928a
1909-30	*Zalophus*	Low	No organized kill but a steady drain from trimming hunters and various collectors	Bonnot, 1931
1913	*Eumetopias*	Moderate	8,000 killed	Townsend, 1918
1927	*Zalophus*	Low	400 adults and nearly every pup on San Miguel Island killed	Bonnot, 1928b
1937-39	*Zalophus*	Moderate	Organized kill for pet food in Mexican waters and perhaps off the coast of California. 180 animals killed per day	Abbott, 1939 and text footnote 4
Late 1920's-1972	*Zalophus*	Moderate to high	Commercial, sport fishing take for interference in fishing operations	Jones, 1981

[1] It was not known whether this was on an annual basis or not.

Literature Review

After a thorough review of the literature, I discovered that few reliable data have been recorded on specific numbers of sea lions harvested in California. However, several papers provide information on the extent of exploitation in a general sense and give some idea of the level to which sealing operations depleted the sea lion population.

The breeding range of *Zalophus* extends south from San Miguel Island (Bartholomew, 1967; Bonnot, 1928b) to the central Mexican coast (Starks, 1921). Rookeries of the Steller sea lion are considered to be from Santa Rosa Island north to the Bering Sea (Bonnot, 1928b; Bartholomew and Boolootian, 1960). These breeding ranges overlap on San Miguel Island (Bartholomew, 1967; DeMaster[1]), and it should be noted that references made in the literature to sea lions during sealing activities in the 1800's and into the early 1900's have not always distinguished between northern and California sea lions.

Sea lions are vulnerable primarily as breeding animals on rookeries and not as nonbreeders on hauling grounds. During the breeding season, they will remain on breeding territories or soon return if driven off. Hauling sea lions will abandon hauling areas if harassed (DeLong[2]). For purposes of simplicity, all animals above Pt. Conception are regarded here as Steller sea lions and those south of Pt. Conception as California sea lions unless otherwise specified in kill records. All animals reported without locations will be referred to simply as "sea lions." Bartholomew and Boolootian (1960) showed that an insignificant percentage of Steller sea lions occurred on southern California islands. Similarly, in censuses when the species were separated, an insignificant number of California sea lions occurred north of Pt. Conception.

Although no population estimates are available from the historical literature, both species of sea lions are reported to have been abundant along the California coast and offshore islands before 1860 (Bonnot, 1928b). In the early to middle 1800's, Russian sea otter hunters and Aleutian Indians used sea lion skins for their canoes, food, oil, and clothing. Reported Ogden (1933), "Every year from . . . 3,600 to 7,200 pounds of sea lion meat were salted down in barrels and boxes." With the advent of commercial harvest, sea lion numbers decreased steadily (Bonnot, 1928a).

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[1] DeMaster, Douglas. 1981. National Marine Fisheries Service, 8604 La Jolla Shores Drive, P.O. Box 271, La Jolla, CA 92038. Pers. commun.

[2] DeLong, Robert. 1981. National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Bldg. 32, Seattle, WA 98115. Pers. commun.

From about 1860 to 1870, thousands of seals and sea lions were harvested for oil (Scammon, 1874).

Scammon (1874) described the commercial products of sea lions; his account gives some idea of the extent of the harvest: "The testes are taken out, and with the selected spires of whiskers, find a market in China, the former being used medicinally, and the latter for personal ornaments." Scammon went on to say that, "a few years ago great numbers of sea lions were taken along the coast of upper and lower California, and thousands of barrels of oil obtained. The numbers of seals slain exclusively for their oil would appear fabulous, when we realize the fact that it requires on an average, throughout the season, the blubber of three or four sea lions to produce a barrel of oil."

If 1,000 barrels is assumed, and a minimum of three sea lions produces one barrel of oil, then these data indicate a take of about 3,000 animals. Assuming 5,000 barrels indicates a take of 15,000 animals. A more extreme estimate of 10,000 barrels increases the estimate to 30,000 sea lions, or 40,000 assuming 4 sea lions per barrel. Scammon indicated that the sea lions were not eliminated on the California shores but would soon be exterminated or "driven away to less accessible haunts."

Whiskers and "trimmings" (the testes and penises of breeding bulls) of California sea lions were still commercially valuable as aphrodisiacs in Oriental trade through the 1930's (Bonnel et al., 1979). Collectors for exhibition and scientific purposes, who worked year-round, were responsible for many California sea lion pup deaths as they took only cows (Bonnot, 1931). The principal cause of the decimation of the Steller sea lion was from the hunters who took them for "trimmings." They killed bulls in such great numbers that Bonnot (1931) expressed his surprise that there were enough left to carry on breeding.

Steller Sea Lion

Isolated accounts of northern sea lions killed in large numbers can be found scattered in the literature. From 1899 to 1902, during the height of the sea lion-salmon fishery conflict, the California State Board of Fish Commissioners requested permission to kill sea lions on Federal lighthouse reservations (Smith, 1902). It was the intent of the Commission to kill 10,000 of the presumed population of 30,000 sea lions along the California coast; however, others more familiar with the sea lion rookeries said this was an overestimation of the population size, which they believed to be less than 10,000 (Merriam, 1902). Permission was granted and soon rescinded due to protests from several Federal agencies, the New York Zoological Society, and various other groups (Bonnot, 1928a, b). The Commission, however, felt its position was justified, and a great many sea lions were killed (Rutter et al., 1902). Bonnot (1928b) reported that several thousand were killed on Año Nuevo.

Townsend (1918) reviewed a report on the sea lion question in British Columbia written by a commission appointed by the Biological Board of Canada. The report covers the years 1915-16. From this report Townsend summarizes that ". . . it appears that a bounty of $2.00 was paid on 4,074 sea lions. It is stated that ' . . . at a conservative estimate there must have been 8,000 killed . . .' " Townsend (1919) later reports on the general negative attitude of salmon packers who destroyed many hundreds of sea lions annually on the Rogue River Reef for several years.

Statistics for numbers of seals and sea lions taken under a bounty system for Oregon and in raiding operations in Queen Charlotte Sound from 1921 to 1926 are reported by Scheffer (1928):

Scalps taken in the state of Oregon:
Eumetopias and *Phoca*

1921-26	8,865

Queen Charlotte Sound during May and June of each year:
Eumetopias

1921-26	7,714
1925-26	1,880 (sea lion pups)

On various occasions sea lions were killed for trimmings. Professional hunters used destructive methods for harvesting; therefore, a significant number of animals killed could not be recovered. As a result, any figures given on the numbers killed anywhere in the country at that time should be supplemented by at least 10 percent in order to arrive at true figures (Bonnot, 1928a, 1931).

From 1927 to 1946 periodic censuses of sea lions were made (Bureau of Marine Fisheries, 1946).

California Sea Lions

Again, specific records of animals killed are sparse and only weakly indicate the extent of commercial harvest for California. Bonnot (1928a) wrote: "Captain H. B. Nidever of San Pedro has supplied me with the information that in 1907 and 1908 several men systematically hunted sea lion bulls at San Miguel Island and killed practically all the bulls of breeding age." Bonnot (1928b) also stated that "a large number of sea lions were killed at San Miguel in violation of the law protecting sea lions in district 19. The methods used by these men would exterminate the sea lions in a few seasons. Bulls, cows and pups were killed indiscriminately . . . ." In addition to "trimmings" hunters, sportsmen, and fishermen, sea lions were taken in unknown numbers by various collectors. From a personal investigation of Flea Island (San Miguel Island), in June of 1927, Bonnot describes the death of every pup of a mixed rookery and of nearly 400 adults. From the late 1920's until the passage of the Marine Mammal Protection Act in 1972, commercial and sport fishermen were allowed to kill sea lions that interfered with their fishing operations (Jones, 1981).

Sea lions were not only exploited for their oil, hides, and "trimmings," but also for use in dog and cat food products (Abbott, 1939; Fry, 1939).

Unpublished Information

If a pet food company used sea lions as a main ingredient in its products before 1972, it was thought that the company(s) might have contract records of the numbers of sea lions procured. Thus, six pet food manufacturers were contacted and representatives of each were questioned about possible use of sea lions in pet food at any time during the company's existence. None were aware of any such use of sea lions or could provide any records of sea lion harvest or purchase.

However, Nathan Lewis, a partner in the Lewis Food Company[3] that bought out Dr. Ross Dog Food in the 1940's was located and supplied the following information: Nathan and his brother D. B. Lewis bought out Dr. Ross at an auction when the company went bankrupt. The company manufactured Skippy and Dr. Ross brand dog food. Nathan Lewis said he believed that Dr. Ross had purchased boats and equipment with the intent to capture sea lions for pet food but failed to pursue this endeavor as his business then went bankrupt.

In Abbott's (1939) account of sea lions killed for pet food, he stated that the harvest occurred on the coast of Mexico under a 20-year concession from the Mexican government. Clinton Abbott was director of the San Diego Museum of Natural History from 1922 to 1946. The Museum's files[4] of Abbott's correspondence on the sea lion slaughter were accessed to uncover further details. The following is information gleaned from these letters that could be pertinent to Channel Island sea lion kill data:

December 1, 1937. To the California Fish and Game Division: Abbott stated that he had received information that the Dr. W. J. Ross Dog Food company was killing sea lions supposedly in Mexican waters. He believed that the Ross company was actually, or at least also, slaughtering sea lions off the coast of California. Abbott had been informed that three boats were operating out of San Pedro and an airplane passing over them counted a large number of seals on their decks. (In his 1939 paper he named the vessels as: the *Romancia*, a killer ship; the *Lotti Bennett*, a tender vessel; and a mother ship, the *F. S. Loop*.)

December 28, 1937. To Dr. W. J. Ross Dog and Cat Food Company: Abbott wrote to the Ross Company and asked many pointed questions about when and how many animals were killed in their operations.

January 10, 1938. To Mr. T. N. Faulconer: Abbott referred to when Mr. Faulconer had given him the names of the cannery boats, operated by Dr. Ross' company, as the *F. S. Loop* and the *Romancia*. He went on to say that the Protective Committee of the American Society of Mammalogists' secretary indicated the boats operating as sealing vessels may have actually been the following: A canning factory ship *California*, U.S. Registry 209117, and two killer boats, *Hawk* 220149 and *Port Saunders* 220150, and that they were killing 180 sea lions per day. There is no information to indicate if Mr. Faulconer was affiliated with an agency or organization.

January 19, 1938. To Mr. Clinton G. Abbott: Dr. Ross replied to Abbott's questionaire by stating the company was in "no position to make any definite statements." The letter did imply the use of sea lions as an "experimental venture."

April 19, 1938. To Abbott from Brazier Howell, Department of Anatomy, Johns Hopkins Medical School, Baltimore, Md: Mr. Howell told Abbott he obtained a figure of 180 sea lions killed per day from a newspaper article.

February 8, 1938. To Abbott from Ing. Miguel A. de Quevedo, Head of the Mexican Conservation Department: de Quevedo assured Abbott that Dr. Ross's annual permit would expire on the 10th of February. (Abbott stated this in his 1939 paper and reported that the slaughter nonetheless was continuing.)

July 13, 1938. To Joseph Grinnell, Museum of Vertebrate Zoology, Berkeley, Calif.: Abbott wrote to Dr. Grinnell that a G. E. Matlock had been hired by Dr. Ross as a "Contact Man." Mr. Matlock had told Abbott that even without a Mexican permit issued to the Ross Company, the Mexicans welcomed the killing of sea lions.

Conclusion

There are few specific data for numbers of California sea lions killed in sealing activities. References in the literature are sparse and inconclusive. Sealing activities on other species of pinnipeds are also poorly documented. Log records, if they exist, of any of Dr. Ross's sealing vessels or other known sealing ships may provide the information needed to begin to estimate the numbers of sea lions killed on San Miguel Island, other Channel Islands, and along the California coast.

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Literature Cited

Abbott, C. G. 1939. Sea lion slaughter. Bird Lore. XLI(193):265-270.

Bartholomew, G. A. 1967. Seal and sea lion populations of the California Channel Islands. *In* Proc. Symp. Biol. Calif. Islands, p. 229-244. Santa Barbara Botanic Garden.

________, and R. A. Boolootian. 1960. Numbers and population structure of the pinnipeds on the California Channel Islands. J. Mammal. 41(3):366-375.

Bonnel, M. L., B. J. Le Boeuf, M. O. Pierson, D. H. Dettman, G. D. Farrens, C. G. Heath, R. F. Gantt, and D. J. Larsen. 1979. (Draft) Final Report, Summary of marine mammal and seabird surveys of the Southern California Bight. III (I) Pinnipeds of the Southern California Bight. Univ. Calif., Santa Cruz, and Bur. Land Manage., 534 p.

Bonnot, P. 1928a. Report on the seals and sea lions of California. Calif. Dep. Fish Game, Fish Bull. 14, 62 p.

________. 1928b. The sea lions of California. Calif. Fish Game 14(1):1-16.

________. 1931. The California sea lion census for 1930. Calif. Fish Game 17(2):150-155.

Bureau of Marine Fisheries. 1946. California sea lion census for 1946. Calif. Fish Game 33:19-22.

Fry, D. H. 1939. A winter influx of sea lions from lower California. Calif. Fish Game 25:245-250.

Jones, R. E. 1981. Food habits of smaller marine mammals from northern California. Proc. Calif. Acad. Sci. 42(16):409-433.

Merriam, C. H. 1902. Food of sea lions. *In* Smith, H. M. 1904. Report on the inquiry respecting food-fishes and fishing-grounds, p. 111-135. U.S. Comm. Fish Fish. Part XXVIII. Rep. Commiss.

Ogden, A. 1933. Russian sea otter and seal hunting on the California coast. Calif. Hist. Soc., Q. 12:29-51.

Rutter, C., R. F. Snodgrass, and E. C. Starks. 1902. Report of the sea lion investigation, 1901, p. 116-119. *In* Rep. U.S. Fish Comm. 1902.

Scammon, C. M. 1874. The marine mammals of the northwestern coast of North America. John H. Carmany and Co., San Franc., 319 p. [Reprinted by Dover Publ. Co., N.Y., 1968.]

Scheffer, T. H. 1928. Precarious status of the seal and seal lion on our northwest coast. J. Mammal. 9:10-16.

Smith, H. M. 1902. Report on the inquiry respecting food-fishes and fishing-grounds, p. 111-135. *In* U.S. Commiss. Fish Fisheries. Part XXVII. Rep. Commiss.

Starks, E. C. 1921. Notes on the sea lions. Calif. Fish Game, 7(4):250-253.

Townsend, C. H. 1918. Sea lions and the fishery industries. N.Y. Zool. Soc. Bull. 21:1679-1682.

________. 1919. The utilization of the sea lion. N.Y. Zool. Soc. Bull. 22:32-33.

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[3] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4] Unpublished correspondence. 1937-1938. San Diego Museum of Natural History Historical Files. San Diego Museum of Natural History, P.O. Box 1390, Balboa Park, San Diego, CA 92112.

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LARVAL GROWTH RATES OF THE PACIFIC SARDINE *SARDINOPS SAGAX* OFF CENTRAL CHILE, DETERMINED BY DAILY RING COUNTS IN OTOLITHS[1]

TASA DE CRECIMIENTO LARVARIO DE LA SARDINA ESPAÑOLA *SARDINOPS SAGAX* FRENTE A CHILE CENTRAL, DETERMINADA POR CONTEO DE ANILLOS DIARIOS EN OTOLITOS[1]

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*John L. Butler**, Javier Chong*, Humberto González*, Ciro Oyarzún* & Carlos Veloso**

ABSTRACT

Growth rates of *Sardinops sagax* (Jenyns, 1842) were determined using counts of daily increments on sagitta otoliths in field collected larvae from the Talcahuano zone (36°35'S; 73°03'W). Size ranged from 5 to 22 mm length that corresponded to an age interval from 3 to 41 days after yolk absorption. Otolith's radius and diameter show an allometric relationship with respect to larval size, and consequently with age. A simple power regression fitted best the data on age and larval size. Growth rates are lower than those reported elsewhere for this species, probably in response to low environmental temperature (12.5°C). Typically *S. sagax* grows 0.4 mm/day when 13.0 mm in size, a rate equivalent to 50% of the rate at 18,6°C. Ecological implications of this finding are discussed.

Key words: Pacific sardine, larvae, growth, daily increments, Chile.

RESUMEN

Se determina la tasa de crecimiento de *Sardinops sagax* (Jenyns, 1842), mediante el análisis de incrementos diarios en otolitos sagitta de larvas recolectadas en el área de Talcahuano (36°35'S; 73°03'W). El rango de tallas estudiado va desde 5 a 22 mm de longitud larval, lo que corresponde a ejemplares de entre 3 y 41 días después de la reabsorción del vitelo. El diámetro y radio de los otolitos se relaciona alométricamente con la talla, y consecuentemente con la edad. Las tasas de crecimiento son menores que las reportadas en otras áreas geográficas para esta especie, probablemente en respuesta a las bajas temperaturas ambientales (12.5°C). Se determina que *S. sagax* crece 0.4 mm/día a los 13 mm de longitud, tasa que equivale al 50% de la tasa de crecimiento a 18.6°C. Se discuten las implicaciones ecológicas de estos resultados.

Palabras claves: Sardina del Pacífico, larva, crecimiento, incrementos diarios, Chile.

INTRODUCTION

After the 1972 "El Niño" (ENSO) phenomenon, that marked the collapse of the anchovy (*Engraulis ringens*) fishery off Perú and northern Chile, the Pacific sardine or "sardina española" (*Sardinops sagax*) extended its geographical range from two refuge areas between Cabo Blanco-Salaverry in Perú and Arica-Mejillones in Chile (Bernal *et al.* 1982). This extension has been suggested as representing a case of ecological replacement among the dominant species in an upwelling ecosystem. In its extension to the south, *S. sagax* has established local populations in several locations. The existence of these local populations can be ascertained by the presence and persistence

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of localized and geographically disjointed spawning areas, with extremely large areas of coast in between where eggs and larvae of this species have not been recorded during the spawning season. Presently the southernmost extension of the geographical range of *S. sagax* has been established in the coastal region of Chiloe island (42°S).

Around Concepción Bay (Talcahuano) and the Gulf of Arauco a spawning center is located, where eggs and larvae of *S. sagax* have been found all year around in significant numbers in the plankton (Herrera, personnal comm.). Reproduction studies in adults, confirm the fact that this species is a serial spawner, and mature individuals have been observed in samples from the fishery throught the year (Aguilera 1984).

Therefore, it seems as a relevant research objective, to study the growth of *S. sagax* in this habitat at temperatures decidedly low and near to the southernmost limit for this species. In order to analyze growth using field information, it is necessary to have an accurate method of ageing the sampled material. Daily growth increments or rings in otoliths provide such a method that has been succesfully used in several fresh-water and marine species.

In this paper the daily otolith ring technique is used to: i) establish a relationship between the size of the sagitta otoliths of *S. sagax* and larval size, in order to make possible back calculations of growth rates; ii) to estimate growth rates of field collected larvae of *S. sagax* in the Talcahuano area (Concepción Bay); and iii) to relate the obtained rates with those obtained for other populations of the same species, and with related species inhabiting other geographical areas.

MATERIALS AND METHODS

Samples for this study were collected during April 1985 (18-IV; 24-IV) from the plankton off Concepción Bay (36°35'S; 73°03'W), with a 0.6 m diameter and 333 μm mesh plankton net, and were preserved in 80% ethyl alcohol. At the station, SST was measured and recorded. Larvae were sorted and identified in the laboratory. Standard (SL) or Notochordal (NL) lengths were obtained to the closest 0.1 mm. Both otic capsules were dissected under 80 X magnification, using polarized transmitted illumination. A pair of polarizing filters (Splindler & Hoyer, Göttingen, FRG) were used, one of which was located between the light source and the specimen, and the second in the light path between the specimen and the scope objective. Rotation of the second filter, allowed the observer to produce almost total interference, point at which the polarized illumination highlighted the otoliths, that could be seen as brilliant, shining objects inside the otic capsules. This very useful optic phenomenon is produced by the bi-refringent nature of the mineral structure of the otoliths.

In all the specimens, at least two otoliths were dissected (right and left sagitta) and mounted on slides using Entellan (Merck T.M.), a synthetic fast mounting medium. Sometimes, more than two otoliths were mounted, when daily growth marks could also be seen on them.

The major axis (diameter, D), and principal radius (the longest distance between the nucleus and the margin, R) of the otoliths were measured under a compound scope to the closest 2.5 μm.

Rings were independently enumerated by two observers under 1000 X magnification. Readings were accepted when they did not depart by 3 units one of each other and the average of the two readings was used. In reporting our results, we followed the practice proposed by Methot & Kramer (1979) wereby "the number of increments (rings) represents the age in days after yolk absorption". Comparisons of growth rates were done considering growth after that developmental event.

In order to check the daily nature of otolith increments, a series of experimentally incubated larvae was obtained from wild collected eggs. Incubation temperature was 12.5 ± 0.5°C under 12 L: 12 D photoperiod. Otoliths from experimentally reared larvae of known age, were dissected and processed similarly than field collected ones.

Non linear regression was performed using BMDP statistical software.

RESULTS

The sagitta is circular when the larvae are small and young (< 7 mm NL). After they reach this size, their growth becomes asymmetrical, developing a major axis and gradually becoming ellipsoidal in shape.

Clear and distinct increments and rings were observed in all otoliths sampled (Plate 1).

Experimentally reared larvae showed otoliths with increments that corresponded to their age in days after yolk absorption. However the rings were less clear than those observed in the otoliths from field collected larvae (Table 1).

Relationships between larval length and either diameter or radius of the otolith, (Figure 1), are best represented by a power curve for the size interval investigated in this study. Table 2 shows the form of the equation fitted and the value of the parameters.

The relationship between age and larval length was best described by a simple power model, that fitted the data with a lower residual sum squares than other kind of regression tested (Figure 2 and Table 3). Growth rates for different size classes are presented in Table 4, where available data for the same or related species are also included.

The observed temperature in the upper layer of the ocean (between surface and 10 m) at collection time was 12.5°C.

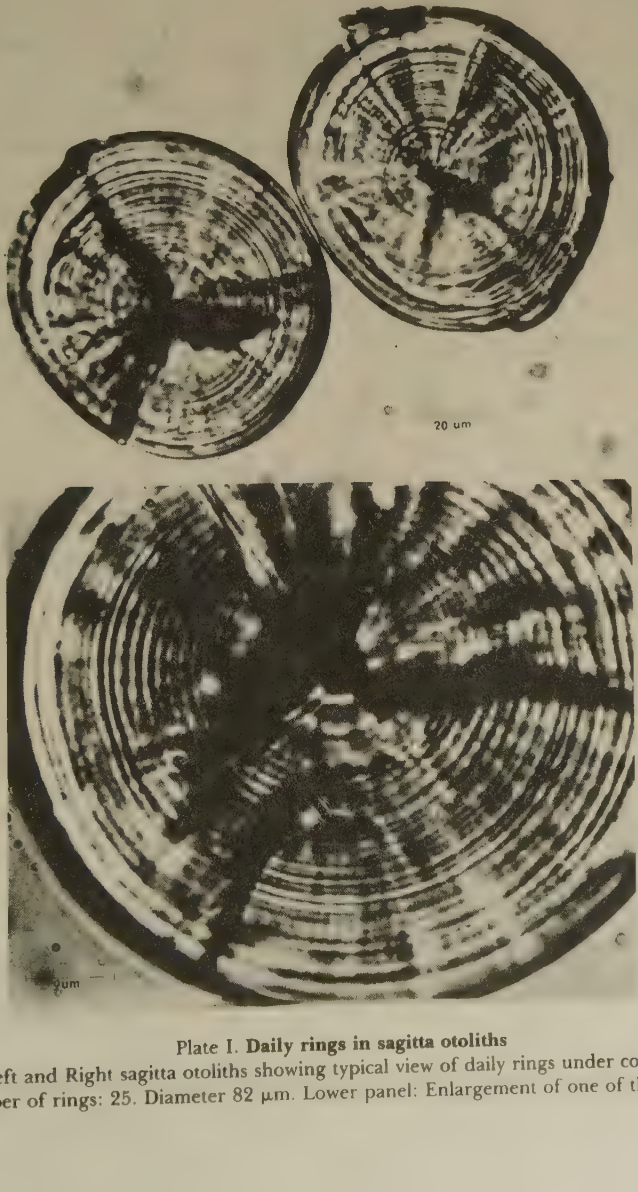

Plate I. **Daily rings in sagitta otoliths**

Upper panel: Left and Right sagitta otoliths showing typical view of daily rings under compound scope. Total number of rings: 25. Diameter 82 μm. Lower panel: Enlargement of one of the otoliths

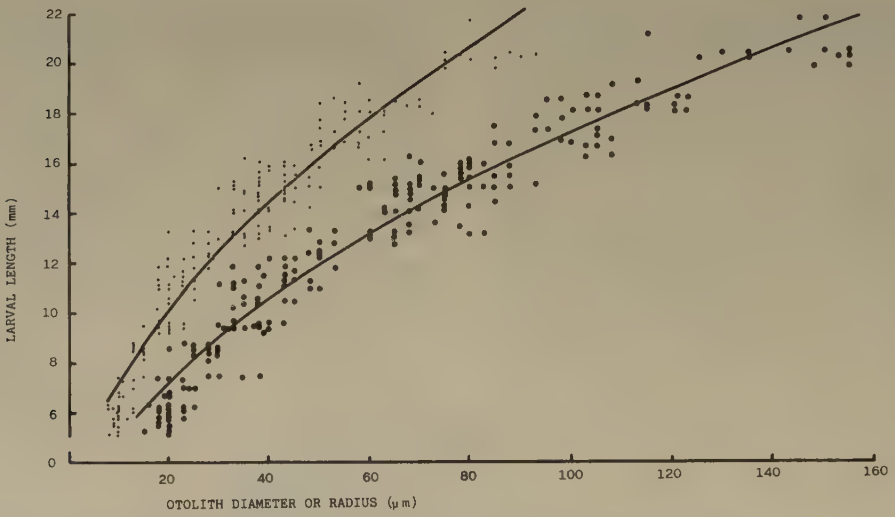

Figure 1. **Relationship between larval length and otolith size.** Small black circles: otolith radius (upper line). Black dots: otolith diameter (lower line)

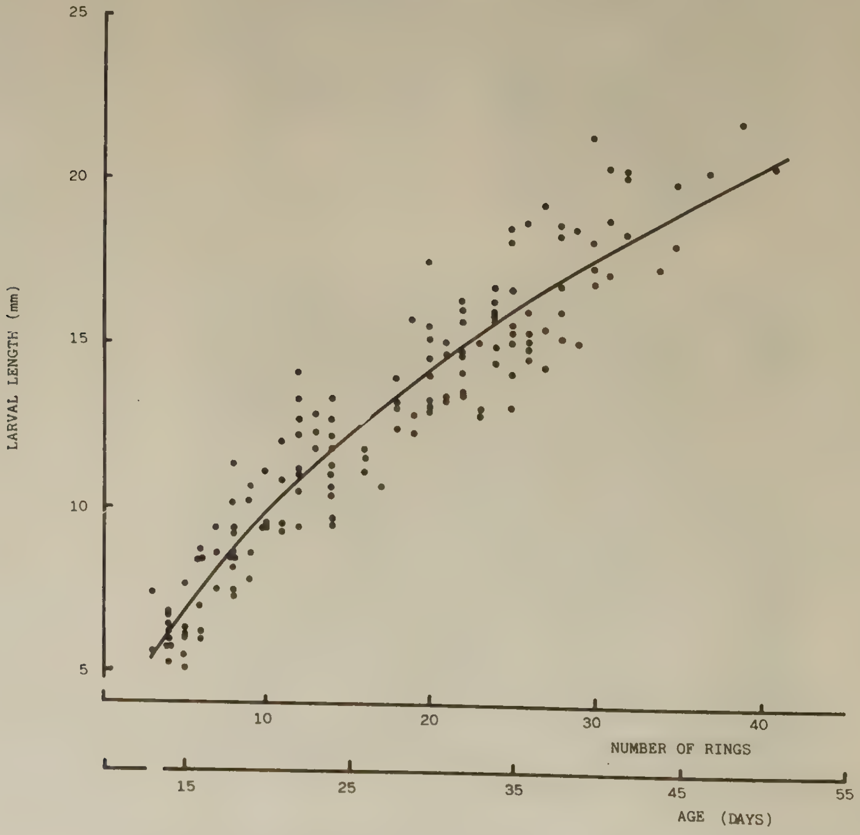

Figure 2. **Power relationship between age (number of rings) and larval length**

TABLE 1
Ring counts from experimentally reared larvae

Age in days after yolk absorption	Number of observations	Average ring number ± 1
1	3	2.0
5	2	6.0
10	6	9.6
14	1	12.0

TABLE 2
Relationship between otolith radius and diameter with larval length

Relationship $Y = ax^b$	Parameters a	b
Otolith radius vs. Length	2.2066	0.5100**
Otolith diameter vs. Length	1.4848	0.5300**

**P < 0.001

TABLE 3
Growth relationships

MODEL		PARAMETERS	RESIDUAL SUM OF SQUARES
Power	$Y = aX^b$	$a = 2.9405$	260.3
		$b = 0.5226$	
Schnute[1]	$Y = \left(a^b + (c^b - a^b) \dfrac{(1-e^{-dx})}{(1-e^{-d100})} \right)^{1/b}$	$a = 1.0000$	267.2
		$b = 0.3771$	
		$c = 25.8196$	
		$d = 0.0398$	
von Bertalanffy[2]	$L = L_\infty (1-e^{-Kt})$	$L_\infty = 50.000$	272.4
		$K = 0.0109$	

[1] Shnute (1981).

[2] L_∞ is only a parameter that describes larval growth. It does not have the conventional meaning.

TABLE 4
Comparison of growth rates for some clupeiform species

Growth rates in mm/day

Species	Size intervals [mm] 5-10	11-15	16-20	21-25	T°C	Reference
Sardinops sagax	1.00	0.75	1.00	0.66	18.6	Butler & Rojas 1985
Sardinops sagax	0.65	0.40	0.29	—	12.5	This study
Engraulis ringens	0.66	0.40	0.30	0.24	12.5	Herrera *et al.*, 1985
Engraulis mordax	0.54	0.67	0.63	—	16.2	Methot & Kramer, 1979
Engraulis mordax	0.33	0.42	—	—	14.4	Methot & Kramer, 1979
Engraulis mordax	0.45	0.48	—	—	13.0	Methot & Kramer, 1979

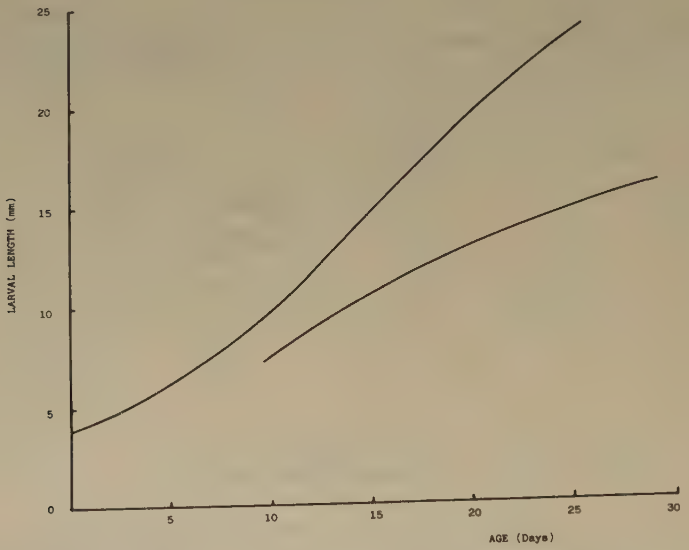

Figure 3. **Comparison of *S. sagax* growth curves at 18.6 and 12.5°C**
Upper Curve: growth curve for Perú at 18.6°C (from: Butler & Rojas de Mendiola 1985).
Lower Curve: Growth curve for Talcahuano at 12.5°C (this study)

DISCUSSION

In order to apply the daily ring method, it is necessary to know at what age is the first ring deposited, and at what rate does the subsequent deposition of rings proceed. We will deal with these assumptions in the same order.

Daily growth marks are first seen on the otolith at certain distance of its geometrical center. Methot & Kramer (1979), working with the northern anchovy (*Engraulis mordax*) have shown that normally the first ring is deposited at the end of the yolk absorption period, and/or when eye pigmentation is completed. Our data for *S. sagax* tend to confirm that in general among clupeiforms, the first ring is formed when the same developmental event is reached, point in time which is a function of temperature. Depending on environmental temperature, this event takes place 3 days after hatching (or 5 days after spawning) at 18°C. Garretón & Balbontín (1982) report that at 12.5°C, yolk absorption is completed 5 days after hatching or 10 days after spawning. Accordingly, it can be assumed that the first ring observed in our samples, corresponds to the 11-th day of life.

Brothers *et al.* (1976) demonstrated the daily nature of ring deposition, by direct examination of larvae of known age of several species. However, in some species such as *Clupea harengus*, some doubt have been cast on the periodical nature of rings (Geffen, 1982; McGurk, 1984). When the appropriate techniques are employed, involving sometimes the use of SEM, the daily nature of increments has been confirmed. The data presented here for the experimentally reared series, confirm the daily nature of the increments for *S. sagax*. It has been assumed that the rate of deposition is constant (one ring/day), an assumption based on the work by Pannella (1971) that demonstrated the daily nature of rings among tropical fishes. More recently it has been demonstrated experimentally, that daily ring formation follows a circadian rhythm controlling the metabolism of calcium, as shown by the level of calcitonin activity and calcium concentration in the blood (Mugiya *et al.* 1981, Butler *et al.* in press).

Sea water temperature at the time of collection (12.5°C), is close to the lowest range of temperature under which development can take place in the laboratory for this species (Garretón & Balbontín 1982), therefore, the growth rates reported here, are low in comparison with what has been observed elsewhere, and might be one of the lowest obtainable for *S. sagax* under natural conditions. Butler & Rojas de Mendiola (1985) reported a growth rate of 0.85 mm/day for *S. sagax* larvae 12.7 mm SL, at 18.6°C in Perú, while off Talcahuano, larvae of equivalent size (11-15 mm SL) are growing 0.40 mm/day at 12.5°C (Figure 3).

Butler & Rojas de Mendiola (1985) suggested that the high growth rate observed for *S. sagax* compared with that of anchovy, could represent "a fundamental ecological difference" for otherwise very similar species. According to these authors, faster growth in *S. sagax* implies a higher ration and hence, at a given food density, larger search volumes, greater swimming speeds and lower predation risk to size specific predators. These advantages are no longer present in the Talcahuano area, and other mechanisms might be acting. *S. sagax*, although a serial spawner over the whole year, shows in Talcahuano a spawning peak during June through September (Aguilera, 1984), the same period for this species in their northern stocks (Chimbote, Arica-Mejillones). This wintry peak is uncoupled with the production cycle in Talcahuano waters, which shows a peak during late Spring and Summer months, while in the north of Chile a close coupling between spawning and production does exist (Retamales & González, 1984, 1985; Bernal *et al.* 1982). As suggested by Butler & Rojas de Mendiola (1985) for the northern stocks, if the differences in growth rates induced by temperature, could contribute to lower competitive pressures between sardine and anchovy, those differences do not exist in Talcahuano during the Fall (this study) and might not exist during the rest of the year due to the small range of variability in temperature.

Our results do not have a simple interpretation in terms of adaptive strategies for the species. Slower growth implies lower rations and longer times to reach the point of no-return, potential advantages for larvae inhabiting poor and cold environments, but also implies, a distinct disadvantage by increasing the duration of one of the most vulnerable stages to predation. The factor that could help to explain the anomalous, off-season, persistance of the "northern timing" in the south, is the reduced predation that could be experienced by the larvae and juveniles spawned in Winter. Evidence in support of this hypothesis, i.e. lower mortality during Winter months, is provided by ichthyoplankton surveys conducted in the northern and southern populations off the chilean coast during Winter and early Summer (Rojas et al. 1983). In Table 5 the average number of eggs and larvae per positive station are compared for each cruise. The ratio of the average number of larvae over the average number of eggs provides a rough index of survival. Comparing the ratios for north and south, it can be seen that in the south there is a ten fold drop from 0.296 to 0.034, suggesting that those larvae spawned in Winter survive better than those spawned in Summer.

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TABLE 5

Relative abundance of eggs and larvae *S. sagax*. Ichthyoplankton survey data

(From: Rojas *et al.*, 1983)

	DATE	No. Stat.	$\bar{X}$ E [+ St.]	$\bar{X}$ L [+ St.]	$\bar{X}$ L / $\bar{X}$ E
SOUTH	81-VIII	87	1402 [18]	415 [43]	0.296
	81-XI/XII	86	1042 [16]	35 [42]	0.034
NORTH	81-VIII/IX	75	2257 [25]	1194 [46]	0.529
	82-II	91	273 [9]	366 [36]	1.341

$\bar{X}$ E Average number of eggs per positive station.
$\bar{X}$ L Average number of larvae per positive station.
[+ St.] Number of positive stations with eggs or larvae.

portunity, the authors of this note participated in a practical training session on the daily ring technique. We would like to than Mr. Victorino Martínez and the crew of M/V Tobago for their help with field work and José Morillas for his help with photographs. Parts of the statistical analysis was performed on the SWFC/UCSD computer center during a visit of G. Herrera to La Jolla sponsored by UNESCO/IOC. The order of the authors was determined by a stratified random sorting.

REFERENCES

AGUILERA, E.A. 1984. Ciclo reproductivo de la sardina española, *Sardinops sagax musica* (Girard, 1854), en el área de Talcahuano. Marine Biologist Dissertation, Universidad de Concepción - Chile, Depto, de Zoología, 83 pp.

BERNAL, P.A., F.L. ROBLES y O. ROJAS 1982. Variabilidad física y biológica en la región meridional del sistema de corrientes Chile-Perú. Monografías Biológicas (Chile), *2*: 75-102.

BROTHERS, E.B., C.P. MATHEWS & R. LASKER 1976. Daily growth increments in otoliths from larval and adult fishes. Fishery Bulletin, .U.S. *74* (1): 1-8.

BUTLER, J.L. & B. ROJAS DE MENDIOLA 1985. Growth of larval sardines off Perú. CalCOFI Reports, *26*: 113-118.

BUTLER J.L., J.E. GRAVES, D. BARTON & L.J. DEFTOS [in press] Diurnal rythms in plasma calcitonin levels of male and female northern anchovy in relation to photoperiod. [Submitted to Transactions of the American Fisheries Society].

GARRETÓN, M. y F. BALBONTÍN 1982. Efecto de la temperatura en el desarrollo embrionario y crecimiento inicial de las larvas de la sardina española, *Sardinops sagax musica* en condiciones de laboratorio. Revista de Biología Marina, Valparaíso, *18* (1): 57-71.

HERRERA, G., E. AGUILERA, G. CASTILLO & P. BERNAL 1985. Growth of anchovy larvae (*Engraulis ringens*) in Central Chile, determined by daily increment counts in otoliths. Biología Pesquera *14*:

GEFFEN, A.J. 1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. Marine Biology, *71*: 317-326.

MCGURK, M.D. 1984. Ring deposition in the otoliths of larval pacific herring, *Clupea harengus pallasi*. Fishery Bulletin, U.S., *82* (1): 113-120.

METHOT, R.D. & D. KRAMER 1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fishery Bulletin, U.S., *77* (2): 413-423.

MUGIYA, Y., N. WATABE, J. YAMADA, J.M. DEAN, D.G. DUNKELBERGER & M. SHIMIZU 1981. Diurnal rhythm in otolith formation in the goldfish, *Carassius auratus*. Comparative Biochemistry and Physiology, *68A*: 659-662.

PANNELLA, G. 1971. Fish Otoliths: daily growth layers and periodical patterns. Science, 173: 1124-1125.

RETAMALES, R. y L. GONZÁLEZ 1984. Fecundidad de sardina española (*Sardinops sagax musica*). Corporación de Fomento de la Producción, Gerencia de Desarrollo. Programa: "Estudio de Recursos Pelágicos", Instituto de Fomento Pesquero, Chile, AP 84-5, 30 pp.

RETAMALES, R. y L. GONZÁLEZ 1985. Incidencia del fenómeno El Niño 1982-83 en el desove de sardina española (*Sardinops sagax*). Investigación Pesquera (Chile) *32*: 161-165.

ROJAS, O., A. MUJICA, M. LABRA, G. LEDERMANN y H. MILES 1983. Estimación de la abundancia relativa de huevos y larvas de peces. Corporación de Fomento de la Producción. Gerencia de Desarrollo. Instituto de Fomento Pesquero, Chile AP 83-31, 98 pp.

SCHNUTE, J. 1981. A versatile growth model with statistically stable parameters. Canadian Journal of Fisheries and Aquatic Sciences, *38*: 1128-1140.

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An Analysis of a Hypothetical Population of Walruses

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ABSTRACT

A series of computer simulations of the Pacific walrus population, using a variable Leslie model, were conducted primarily to test the hypothesis that the population increased from about 70,000 in 1955 to about 200,000 in 1975 and, secondarily, to evaluate the reliability of the data available on adult survival rates. Published estimates of the population size, the sex ratio of adults, age at sexual maturity, average reproductive rate, adult mortality, and size and sex/age composition of the annual harvests were incorporated into the model. The results suggested that, either the estimates of size of the 1955 population were too low, or that the survival rates of adults were significantly higher than believed. They suggested further that an increase to 200,000 in 20 yr would have been possible, if the initial population in 1955 had been made up of about 94,000 to 98,000 animals, the sex ratio of adults was 1 male:3 females, and the adult survival was 0.96, with nonlinear density dependence. Such an increase would have been impossible with linear density dependent functions, smaller initial population size, or lower adult survival rates. The maximum sustained yield (MSY) of the hypothetical population, assuming continuation of the current harvest composition at 3 males:1 female, would be between 3 and 5% and should be available when the population is between 59 and 91% of the carrying capacity (*K*), assuming environmental stability. The maximum net productivity (MNP) of this hypothetical population was estimated to be attained at 50 to 84% of *K*.

РЕЗЮМЕ

Моделирование на счетно-решающем устройстве было произведено с помощью «переменной модели Лесли», главным образом, чтобы проверить гипотезу об увелечении численности тихоокеанского моржа приблизительно с 70,000 в 1955 г. до 200,000 голов в 1975 г., а также оценить надежность имеющихся данных о способности выживания взрослых зверей. Опубликованные данные по оценке величины популяции, половому соотношению взрослых, возрасту полового созревания, среднему темпу воспроизводства, смертности взрослых, возрастному составу и ежегодной добычи использовались в модели. Результаты дают основание предполагать, что величина популяции в 1955 г. была слишком низкой или темп выживания взрослых был гораздо выше, чем это считалось ранее. Кроме того, результаты позволяют предпологать, что увеличение до 200,000 голов в течение 20 лет было бы возможным, если популяция в 1955 г. составляла 94 - 98,000 голов, половое соотношение взрослых 1 самец: 3 самки и выживание взрослых - 96% с нелинейной плотностью зависимости. Такое увеличение было бы невозможным с линейной плотностью зависимости, меньшей первоначальной величной популяции, или низким выживанием взрослых. Максимальная ежегодная добыча гипотетической популяции, при сохранении в добыче соотношения 1 самка: 3 самца, будет составлять 3 - 5%. Такой уровень добычи возможен, если при максимальной плотности саморегулирующейся популяции [*K* = 59 - 91%] и стабильности экосистемы. Считаем, что максимальное чистое производство этого гипотетического населения достигается при 50 - 84% *K*.

По оценке автора максимальная чистая продуктивность данной гипотетической популяции может быть достигнута при *K* = 50 - 84%.

INTRODUCTION

In the late 1950's, the size of the Pacific walrus, *Odobenus rosmarus divergens*, population was considered to have been between 40,000 and 70,000 animals (Fay 1957; Kenyon 1960;[2] Fedoseev 1962). Nevertheless, Kenyon (footnote 2) felt that the actual population size in the late 1950's may have been higher than 70,000. Estes (1976),[3] Estes and Gilbert (1978), and Estes and Gol'tsev (1984) supported Kenyon's judgement with evidence that Fay and Fedoseev had underestimated the number of walruses in the American sector of the Chukchi Sea. More recent estimates of the Pacific walrus population have placed it at 140,000 to 200,000 (Estes and Gol'tsev 1984) and 168,000 to 250,000 individuals (Krogman et al. 1978[4]). Estes and Gilbert (1978) concluded that estimates produced from limited aerial surveys should not be considered reliable.

Perhaps the best quantitative information available concerning the Pacific walrus population is contained in the American and Soviet harvest data from 1959 to 1975 (Harbo 1961;[5] Burns 1965[6]

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[1] National Fish and Wildlife Laboratories, U.S. Fish and Wildlife Service, Anchorage, Alaska; present address: Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, USA.

[2] Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. Unpubl. rep., 39 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

[3] Estes, J. A. 1976. The reliability of aerial surveys to estimate population abundance of marine mammals. Consideration from a survey of Pacific walrus. Scientific Consultants on Marine Mammals, Bergen, Norway. 31 August-September 1976. [FAO] Advis. Comm. Mar. Resour. Res. ACMRR/80, 13 p.

[4] Krogman, B. D., H. W. Braham, R. M. Sonntag, and R. G. Punsly. 1978. Early spring distribution, density, and abundance of the Pacific walrus (*Odobenus rosmarus*) in 1976. Final report R.U. 14, 47 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

[5] Harbo, S. J., Jr. 1961. Walrus harvest and utilization. Annual project segment report, Federal Aid in Wildlife Restoration. Alaska Dep. Fish Game, Juneau, 25 p.

[6] Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Dep. Fish Game, Juneau, 48 p.

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and unpubl. data; Krylov 1968; F. H. Fay[7]). These data include the retrieved kill and estimated losses from wounding and sinking; for the American harvest, they also include the sex ratio of adults and the number of calves taken. Studies of the reproductive organs from the harvested animals have produced estimates of age-specific rates of fecundity (Fay 1960;[8] Burns footnote 6; Krylov 1968), but these estimates generally have not been accepted due to suspected sampling bias in the harvests and in the assumptions of the estimation process.

To date, then, "relatively" reliable information exists on the size and sex/age composition of the Alaskan walrus harvests from 1955 to 1975, and on the age-specific rates of reproduction. Only the total harvests are known from the Soviet side. The estimates of population size in 1955 to 1975 are questionable, and the estimated rates of natural mortality appear to be unreliable. Nevertheless, these were the best figures available and of sufficient quality for use in a preliminary computer model of the Pacific walrus population.

The primary purpose of integrating the existing estimates of population parameters into the format of a computer model was to test the hypothesis that the Pacific walrus population could have increased in size from 70,000 to 200,000 animals in the 20 yr from 1955 to 1975. Such a model can be used also to estimate unknown parameters, when all others are fixed, and to assess the reliability of any that are in question. In addition, the interrelationships between the various parameters can be examined, and a better understanding can be gained of the relative importance of each to the population.

Table 1.—Parameters used in the population models, where m_x is the age specific reproductive rate, and p_x is the age specific survivorship.

Age	m_x	p_x	Age	m_x	p_x
0	0	0.94	20	0.22	0.96
1	0	.90	21	.22	.96
2	0	.94	22	.22	.96
3	0	.96	23	.22	.96
4	0	[1].96	24	.22	.96
5	0.10	.96	25	.15	.96
6	.12	.96	26	.15	.96
7	.17	.96	27	.15	.96
8	.22	.96	28	.15	.96
9	.22	.96	29	.15	.96
10	.22	.96	30	.15	.96
11	.22	.96	31	.15	.96
12	.22	.96	32	.15	.96
13	.22	.96	33	.15	.96
14	.22	.96	34	.15	.96
15	.22	.96	35	.15	.96
16	.22	.96	36	.15	.96
17	.22	.96	37	.15	.96
18	.22	.96	38	.15	.96
19	.22	.96	39	.15	.96

[1]Survival from age 4 and older assumed to be density dependent. All other parameters are assumed constant.

Table 2.—Assumed parameters for estimation of adult survival necessary for the population to increase from 70,000 to 200,000 in 20 yr.

Parameter	1955	1975
Female population	52,500	150,000
Total population	70,000	200,000
Sex ratio	1♂:3♀	1♂:3♀
Female kill	1,675	1,675
Total kill	6,700	6,700
Sex ratio of kill	1♀:3♂	1♀:3♂

METHODS

The population model used in this instance was a modification of Leslie's (1945) model, as described by DeMaster (1981); similar models were described by Fowler and Smith (1973) and by Fowler and Barmore (1977).[9] The model assumes that the influence of density dependence on the life history parameters will be within the range of the following two types of functions:

$$Pi = A - c\,N_x \qquad \text{(linear)}$$

$$Pi = A\,(1-\exp[-b\,(k-N_x)]) \qquad \text{(nonlinear)}$$

where Pi = annual survival of the ith age class
A = maximum annual survivorship
N_x = number of females 4 yr old and older
k = maximum number of females 4 yr old and older
b = constant associated with the shape of the curve
c = constant associated with the slope of the curve.

The initial values for the projection matrix (Tables 1, 2) were derived from the American and Soviet data. Only the female segment of the population was incorporated into the model; the sex ratio was assumed to be constant at 1 male:3 females (Fay 1982). The initial population vector was calculated by solving the following equation for N_0, the number of female calves in the initial population:

$$P = N_0 + .94\,N_0 + (.94)(.90)N_0 + (.94)^2(.90)N_0 + \sum_{x=1}^{36}(.94)^2(.90)(.96)^x$$

where P = 52,500, the number of females in a population of 70,000 walruses. Subsequent age classes were calculated by using the age-specific survival rates from Table 1.

The number of females 4 yr old and older (k) in the maximal population of about 200,000 walruses (Fay 1957) was assumed to be 150,000. The constant b was arbitrarily set at 0.002, which represents a relatively rapid change in the shape of the nonlinear function (Eberhardt and Siniff 1977). The constant c was set at 0.0000007, which was calculated directly from the nonlinear model as the slope between the two points described by the survivorship and the population at equilibrium, given an initial survivorship of 0.96 at a population level of 0 (DeMaster 1981). In this way, the simulations with linear and with nonlinear density dependence had the same equilibrium population.

The population model assumed that only animals 4 yr old and older were harvested. The harvest of a particular age class was weighted in proportion to the frequency of occurrence of that age class in the harvest data. Compensatory and additive harvests were represented by the following equations (DeMaster 1981):

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[7] F. H. Fay, Associate Professor, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. October 1979.

[8] Fay, F. H. 1960. Investigations of the Pacific walrus. Terminal report, Project 26. Arctic Institute of North America, Montreal, Canada, 72 p.

[9] Fowler, C. W., and W. J. Barmore. 1977. A population model of the northern Yellowstone elk herd. *In* R. M. Linn (editor), Proceedings First Conference on Scientific Research in the National Parks, New Orleans, Louisiana, November 9-12 1976. Vol. 1, p. 427-434

harvest mortality additive:

$$X\ (i+1) = L[X\ (i) - H\ (i)],$$

harvest mortality compensated for:

$$X\ (i+1) = L[X\ (i) - H\ (i)],$$

where $X\ (i)$ = the population vector at time i
L = the projection matrix
$H\ (i)$ = the harvest vector.

Using this model, a series of simulations was computed in which the maximum annual survivorship (A) was increased in each simulation until the population model produced the desired final size. The total kill of females was assumed to be constant over the 20-yr period. The average kill was derived from known harvest data.

RESULTS

The hypothetical population, given a nonlinear density dependent function, increased from 70,000 to 200,000 in 20 yr only when A, the annual survivorship, was set to equal 0.99. This value of A was necessary whether or not the harvest mortality was compensatory. The simulated population, given a linear density dependent function, could not increase from 70,000 to 200,000 in 20 yr, even when A was set at 1.00.

Because the natural rate of adult survival probably could not have been as high as 0.99 to 1.00, one must assume that some other component of the model is incorrect. For the reasons given by Estes and Gilbert (1978), the most questionable component is the initial size of the population. Given the entries for the projection matrix from Tables 1 and 2 (excluding initial population size), nonlinear density dependence, and a harvest mortality that was additive, the initial population of females would have had to have been 73,828 (total population 97,828) to have produced the hypothetical final population of 200,000 in 20 yr. If the harvest mortality was assumed not to be additive, an initial population of 70,645 females (total population 94,194) would have been necessary for the increase to 200,000. If the form of the density dependent function was assumed to be linear, initial populations even of these sizes could not have reached 200,000 in 20 yr, given an adult female harvest of 1,675/yr.

In the United States, the Marine Mammal Protection Act of 1972 (MMPA) dictates that marine mammals should be managed at the level of "optimum sustainable population" (OSP). The concept of OSP is interpreted to mean that the population should remain between an upper level imposed by environmental constraints (commonly called K) and a lower level at which the population would produce the greatest annual increment (maximum net productivity = MNP) if the population were not being harvested. To estimate this lower level directly from a population that is being harvested is impossible, but it can be estimated through modeling. Given the age specific rates of births and deaths in Table 1 and the nonlinear density dependent function previously described, the MNP of the simulated population would occur at 84% of K, the equilibrium population (Table 3). For simulations with linear density dependence, the MNP would occur at 50% of K. If we assume that the real MNP is within the range of these two forms of density dependence, the lowest level of the population that would be acceptable under the MMPA would be between 50 and 84% of K.

Table 3.—Comparative dynamic characters of walrus population models with linear and nonlinear density dependence.

Character	Density dependence	
	Linear	Nonlinear
Maximum net productivity (MNP)	50% of K	84% of K
MSY (no compensation)	2,100 adult females	6,800 adult females
Population at MSY_{nc}	59% of K	86% of K
MSY (compensation)	2,200 adult females	7,400 adult females
Population at MSY_{c}	59% of K	91% of K

Current information on the Pacific walrus population suggests that it has increased dramatically since 1955. Within the guidelines of the MMPA, the population could conceivably be managed somewhere between K and the MNP levels. As a starting point, the maximum sustainable yield (MSY) of a specific segment of the population can be estimated, but only if various age and sex specific life history parameters are known. In addition, how these parameters respond to changes in density must be known. Even then, the estimated MSY is only reliable if the environment is relatively constant. To estimate the MSY of adult female walruses, a series of simulations were computed, in which the harvest was continually increased, until the population no longer could sustain it (DeMaster 1981). Using the life history parameters of Table 1 and a nonlinear form of density dependence, the MSY of adult females (females 4 yr and older) would be 5.1% of the total population of females, and would occur at 91% of K (Table 3). If the density dependent function was assumed to be linear, the MSY of adult females would be 2.3%, and would occur at 59% of K. Obviously, we do not know the proper form of the density dependent function, but these results suggest that an adult female harvest of 2 to 5% could be sustained, and presumably would result in the population reaching an equilibrium when it was between 59 and 91% of K.

DISCUSSION

The exact details of the recovery of the Pacific walrus population are not known, but at least a partial recovery has taken place (Burns footnote 6; Fay footnote 8; Estes and Gilbert 1978; Estes and Gol'tsev 1984). This recovery has occurred in spite of a continual harvest of adults. The average growth rate necessary for a population to double in 20 yr is 1.035, and to triple in 20 yr is 1.056. Such rates of growth are common for many species of marine mammals (Eberhardt and Siniff 1977), but seem somewhat improbable in this instance, considering the low productivity and ongoing harvest of Pacific walruses.

The purpose of this paper was to produce a model that would incorporate the existing data and shed some light on the reliability of the estimate of population size in 1955 and the estimated rate of annual mortality. The results from the various simulations suggest that, either the natural rate of adult mortality is extremely low relative to other pinnipeds (Eberhardt and Siniff 1977), or that the population estimate for 1955 was too low.

The model described in this paper was based on numerous assumptions for which substantive data are few and, in some cases, questionable. In all of the simulations, I assumed that the sex ratio of the adult population remained constant at 1 male:3 females, based on Fay's (1982) derivations from shipboard visual and aerial photographic surveys of the Pacific walrus population. Further information on herd composition and how it varies throughout the year is needed for improvement of the estimate of adult sex ratio. Simulations in which the sex ratio is assumed to be 1:2 and 1:1 also should be computed. The effect of these would be to increase the difference between the estimated and required population in 1955, given the life history values of Table 1. Increasing this difference will only strengthen the argument that either the 1955 population estimate was too low or that estimates of adult survival were too low. Second, I have assumed that the environment of the walrus remained relatively constant. Although human perturbation (other than hunting) probably has been minimal over the past 20 yr, natural perturbations may have occurred and not been recognized.

In all of the simulations where a harvest took place, I assumed that the sex ratio of the harvest was 3 males:1 female, and that a constant number was taken each year. Data concerning the sex ratio of the harvest supports a 1:3 ratio (Burns footnote 6; Fay footnote 8), but the numbers taken were not constant; rather, they declined from about 9,000 in 1955 to about 3,000 in 1969, and have been rising slowly since then to about 7,000. The effects of these changes on the population probably were insignificant, if the initial harvests were low enough to allow the population to increase (which, apparently, it did).

Data on the kinds of density dependent factors influencing this population were not available at this writing. Simulations which incorporate density dependent reproduction or calf survival should be computed.

Evidence from Weddell seals, *Leptonychotes weddelli*, suggests that reproduction may be relatively unaffected by changes in density, because the time of reproduction does not coincide with the seasonal onset of poor feeding conditions (DeMaster 1981), and this may be the case for walruses as well. One could assume that all independent walruses will be affected equally by food shortages, and that younger individuals will not be more disadvantaged than the older ones in obtaining food. The advantages usually invoked for older pinnipeds, such as greater experience with the area, better diving capabilities, and outright dominance, may not apply under conditions where all feeding is done in relatively shallow waters, the distribution of the ice dictates which areas can be utilized, and a major portion of the adult males may not be feeding in the same areas where the subadults and adult females feed. Obviously more information is needed on these points.

Throughout this paper, a distinction has been made between natural mortality and mortality due to harvests. One problem that arises in estimating mortality rates from age composition of the harvest is that mortality from both sources is combined. Furthermore, estimates of mortality derived from samples of populations that are growing will be biased upward (Payne 1977). Burns (footnote 6) suggested that adult male mortality was about 13%/yr, based on the age fecundity from the harvest. If the Pacific walrus population was growing at about 5%/yr, the estimate of survival from age composition will be negatively biased (Payne 1977). When corrected as:

$$S = e^{(\ln .87 + \ln 1.050)} = .91$$

where S = annual survivorship, the better estimate for adult male mortality would be 9%/yr. Again, this includes both natural and hunting mortality. If the Pacific walrus is polygynous (Fay et al. 1984), and the harvest of males is greater than that of females, the rate of natural mortality for adult females should be less than the total mortality for adult males, rather than greater as indicated by Burns (footnote 6). Therefore, the male mortality rate of 13% (Burns footnote 6) should exceed the maximum for adult females, the actual rate probably being much lower.

All of the simulations in which the population increased as rapidly as hypothesized (3 to 5%/yr) required that natural adult survivorship be above 95%, given the known level of harvest. The model suggests that the Pacific walrus population was theoretically capable of increasing from 70,000 to 200,000 in 20 yr, but to have done so, the sex ratio of the population would have had to have been strongly weighted to females. Information on the current sexual composition of the population would, therefore, be extremely useful for better understanding of the population dynamics of this species.

Finally, the model suggests that the MNP of a population varies considerably with the type of density dependence that is operative. This has been demonstrated also for MSY values (DeMaster 1981). MNP values for marine mammals commonly are assumed to lie between 50 and 60% of *K*. More realistic estimates of MNP will require information on the age at which density related changes take place in life history parameters, and on the form of the relationship between life history parameters and density of the population.

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LITERATURE CITED

DeMASTER, D. P.
1981. Incorporation of density dependence and harvest into a general population model for seals. *In* C. W. Fowler and T. D. Smith (editors), Dynamics of large mammal populations, p. 389-401. Wiley-Interscience, N.Y.

EBERHARDT, L. L., and D. B. SINIFF.
1977. Population dynamics and marine mammal management policies. J. Fish. Res. Board Can. 34:183-190.

ESTES, J. A., and J. R. GILBERT.
1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). J. Fish. Res. Board Can. 35:1130-1140.

ESTES, J. A., and V. N. GOL'TSEV.
1984. Abundance and distribution of the Pacific walrus, *Odobenus rosmarus divergens*: Results of the first Soviet-American joint aerial survey, autumn 1975. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:67-76.

FAY, F. H.
1957. History and present status of the Pacific walrus population. Trans. North Am. Wildl. Nat. Resour. Conf. 22:431-443.
1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North Am. Fauna 74, 279 p. U.S. Fish Wildl. Serv., Washington, D.C.

FAY, F. H., G. C. RAY, and A. A. KIBAL'CHICH.
1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:89-99.

FEDOSEEV, G. A.
1962. On the status of the stocks and the distribution of the Pacific walrus. Zool. Zh. 41:1083-1089.

FOWLER, C. W., and T. SMITH.
1973. Characterizing stable populations: an application to the African elephant population. J. Wildl. Manage. 37:513-523.

KRYLOV, V. I.
1968. Present condition of Pacific walrus stocks and prospects of their rational exploitation. *In* V. A. Arsen'ev and K. I. Panin (editors), Pinnipeds of the northern part of the Pacific Ocean, p. 189-204. Pischevaya Promyshlennost', Moscow.

LESLIE, P. H.
1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

PAYNE, M. R.
1977. Growth of a fur seal population. Philos. Trans. R. Soc. Lond. 279:67-79.

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7. Conflicts between marine mammals and fisheries off the coast of California

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Introduction

Marine mammal–fishery interactions can result in both revenue losses to fishermen and mortality of marine mammals. These interactions can involve damage to captured fish, damage to nets and gear, reduced catch rates due to scaring of target species, reduced availability of target species, and incidental entanglement. The purpose of this chapter is to describe two research projects that have been supported by the National Marine Fisheries Service to document the nature and extent of marine mammal–fishery interactions in California. The first project was contracted out to the California Department of Fish and Game, and was directed by Dan Miller (California Fish & Game, Monterey office). The second project is part of the research programme of the Coastal Marine Mammal Project (Southwest Fisheries Center, La Jolla, California). This study, the cooperative Marine Mammal Salvage Program, was originally headed by John Hendersen, and is currently directed by Larry Hansen.

Marine mammal–fisheries interaction study

Beginning in July 1979, the Southwest Fisheries Center and the Southwest Regional Office of the National Marine Fisheries Service jointly sponsored a contract with the California Department of Fish and Game to determine the nature and extent of interactions between marine mammals and all commercial and recreational fisheries in California. The results of the first year of this study are summarised in an annual report (Miller 1981), and a summary of its first two years is given Miller *et al.* (1982) and Herder (1982).

In this contract, an effort was made to determine the loss of fish and damage to gear due to marine mammals by questioning fishermen who had recently completed trips and by sending out observers on fishing trips when possible. In addition, an effort was made to monitor the incidental take of marine mammals in various fisheries. Miller (1981) reported that there was considerable concern on the part of the gill-net and trammel-net fishermen and salmon trollers that information on incidental take of marine mammals may eventually curtail their operations. Estimates of fish loss and gear damage were generally available for all fisheries, whereas estimates of marine mammal take were not available for most fisheries.

Seven fisheries were identified in which a consistent loss of fish and/or damage to gear was occurring (Table 7.1): the commercial salmon trolling fishery, the California

Table 7.1 The value of fish and gear depredated by marine mammals annually (data from Miller *et al.* 1982).

Fishery	Fish lost ($)	Gear lost ($)	Total ($)
Salmon fisheries			
commercial troll	274 000	12 220	286 220
commercial sport boat	6 000	360	6 360
skiff	2 300	0	2 300
Klamath River – subsistence	74 000	10 000	84 000
Total salmon	365 300	22 580	378 880
sport boat non-salmon	27 000	10 730	37 730
Pacific herring	57 100	4 550	61 650
Gill-net	63 360	57 070	120 430
Total fisheries	503 760	94 930	598 690

halibut gill-net fishery, the Native American gill-net fishery in the Klamath River, the commercial sport-boat fishery out of San Diego, the Pacific herring fishery, the partyboat and skiff salmon fisheries, and the round-haul fisheries for anchovy and mackerel. In addition interactions between the southern California squid fishery and California sea-lions and short-finned pilot whales were described (Miller *et al.* 1982), but financial losses were not quantified. Significant interactions with marine mammals were not observed in the following fisheries: the pier fishery, the shoreline hook-and-line sport fishery, the bottomfish skiff fishery, the partyboat bottom-fish fishery north of Morro Bay, the lamprey fishery of the Eel and Klamath rivers, the night and surf smelt fisheries, the bottom-trawl fishery, the lobster fishery, and the swordfish spearing fishery.

The largest financial loss due to interactions with marine mammals was reported from the commercial salmon trolling fishery. A minimum loss of $130 000 during the month of May 1980 was estimated. This estimate does not include losses due to gear damage. The total value of salmon landed in California during May was about $5 000 000. Miller *et al.* (1982) reported that roughly two-thirds of the total value of fish and gear lost due to marine mammals occurred in this fishery (Table 7.1).

The marine mammal species primarily involved in the salmon fishery interactions is the California sea-lion (*Zalophus californianus*). During the 113 observed trips made in 1979–80, only one sea-lion was shot at. Miller (1981) reported that more animals were probably taken in 1979 than are indicated by this one observation. The annual loss of salmon from the recreational catch and from the skiff fishery was much less than for the ocean salmon fishery (Table 7.1).

Miller (1981) reported that the Klamath River Native American (subsistence) gill-net fishery was the most difficult fishery to monitor. He also reported that this is the fishery that is thought to be most affected by marine mammal predation. Harbour seals (*Phoca vitulina*) have been observed to remove netted salmon quickly from the nets (Miller 1981). Entanglement of harbour seals in nets was observed, as well as harbour seals and California sea-lions being shot near the nets (Miller 1981). Herder (1982) reported that roughly 926 salmonids were damaged out of a total harvest of 6800

(14%). If fishermen were to replace these with market fish, this would represent a total loss of roughly $84 000, or $2400 per fisherman.

Losses to marine mammals from the commercial sport-boat fishery were negligible in central California, roughly 2.5% of the total catch in southern California, and over 6% in Baja California (Miller 1981). This loss was primarily due to predation by California sea-lions. The estimated losses computed from definite loss values varied between 15 141 fish and 18 272 fish (Miller *et al.* 1982). Pacific bonito was the most frequently lost fish. Other fish lost included: Pacific mackerel, kelp bass, California barracuda, and several species of rockfish. The value of fish and gear loss in southern California varied between $37 000 and $38 800.

The gill-net and trammel-net ocean fisheries were also significantly impacted by marine mammal predation. In waters off Baja California, 12.5% of the catch was lost to sea-lion predation (Miller 1981). In southern California waters, the estimated fish loss was 2.2%; most of this loss was due to California sea-lions. Losses occurred in the following fisheries (Miller *et al.* 1982): shark drift gill-net fishery ($1400), California halibut gill-net and trammel-net fishery ($72 700; depredation rate of 10.1%), white seabass gill-net fishery ($7980; depredation rate of 10.4%), rockfish set-gill-net fishery ($18 060; depredation rate of 1.6%), white croaker gill-net fishery ($3978; depredation rate of 7.1%), and Pacific bonito gill-net fishery ($1652; depredation rate of 6.5%).

The Pacific herring fishery was difficult to monitor because nets are fished both day and night and are often left unattended. Both California sea-lions and harbour seals have been observed foraging on netted fish. In this fishery, damage to the gear (the nets) may be more significant than loss of fish. Three different types of nets are used in this fishery: gill-nets, lampara nets, and purse-seine nets. Fishermen in this fishery are more concerned with sea-lions frightening fish out of the nets than they are with the actual number of fish eaten by sea-lions that enter nets (Miller *et al.* 1982).

The dip-net squid fishery of southern California was estimated to have lost over $36 000 due to interactions with California sea-lions and short-finned pilot whales (*Globicephala macrorhynchus*) in 1980 (Miller 1981). Fish in the catch are not eaten, but the frightening of squid away from the dip-net area results in a considerably lower catch per unit effort. The squid fishery in Monterey primarily uses lampara nets, and

Table 7.2 Comparison of percentage of catch lost to marine mammal predation from interviews with fishermen and from observed trips at sea. (Figures in parentheses indicate numbers of fish.)

	Data source	
Fishery	At sea (%)	Interviews (%)
commercial salmon (ocean)	2.4 (113)	3.2 (1506)
partyboat salmon	0.64 (72)	1.35 (157)
partyboat salmon	0.0 (13)	0.0 (20)
partyboat bottomfish		
gill-net and trammel-net (bottomfish)		
southern California	0.7 (35)	2.2 (125)
central California	0.0 (5)	2.4 (13)

interaction with marine mammals is relatively rare. The potential for frightening off fish and foraging by marine mammals in the round-haul net fishery for anchovy and mackerel was reported to be high. Data are currently not available on the value of the fish lost, but efforts are underway to determine this.

Miller (1981) provided information on fishery–marine mammal conflicts from at-sea trips and from interviews. A comparison of these techniques is currently underway. However, a preliminary comparison of these two data sets indicates that data from interviews will generally give higher estimates of fish lost to marine mammals than will data from at-sea trips (Table 7.2). Subsequent analyses will need to identify factors that may be contributing to differences between these two sampling techniques. One interpretation of these results is that fishermen overestimate the loss of fish due to marine mammal predation. An alternative hypothesis is that fishermen may be fishing differently when observers are on board. Obviously, many other hypotheses can be generated, and more information is needed to test any of them.

Marine mammal mortality in California fisheries

Miller *et al.* (1982) estimated that 300 California sea-lions were taken each year by shooting in the commercial salmon trolling fishery (Table 7.3). This was determined by interviewing fishermen. There were no reported mortalities of marine mammals associated with the commercial salmon sport-boat fishery, the recreational skiff fishery for salmon, the non-salmon commercial sport-boat fishery, or the Pacific herring fishery. In the shark drift-gill-net fishery, 49 California sea-lions were entangled in 177 at-sea days sampled (Miller *et al.* 1982). This represents a mean catch rate of 0.28 ±0.19 California sea-lions per net-night. Other marine mammals 'taken' included two short-finned pilot whales, three grey whales (*Eschrichtius robustus*), and one baleen whale, but the interaction rates were too low to quantify. Miller *et al.* (1982) estimated that between 678 and 1227 sea-lions were drowned between September 1980 and September 1981 in shark drift gill-nets. Mortality was also reported in the shark set-gill-net fishery and the California halibut gill-net and trammel-net fishery. No mortality was observed in the white sea bass, rockfish, white croaker, California barracuda, Pacific bonito, or flyingfish fisheries (Miller *et al.* 1982), but a few entanglements were reported by fishermen.

In the Monterey Bay halibut gill-net fishery, the estimated marine mammal mortality in June 1980 was 45 California sea-lions, 15 harbour seals, and 15 harbour porpoise (*Phocoena phocoena*). These numbers were determined after 25 days of at-sea observations. No additional marine mammal mortality was reported for the rest of the year (20 observer-days reported by Miller *et al.* 1982). In June 1981, Miller *et al.* (1982) estimated mortalities of 22 harbour seals and 22 California sea-lions. The pinnipeds in 1980 and 1981 were juveniles (Miller *et al.* 1982). In May of 1982, this fishery moved north into Bolinas Bay. D. G. Ainley *et al.* (personal communication) reported that a large number of birds, 13 harbour porpoise and 15 harbour seals were found along a 40-mile stretch of coast. Of the 13 harbour porpoises found, 7 were 'fresh'; 4 had obviously been captured in nets. Historically, the number of stranded harbour porpoises averages 2.1 animals per year, a much lower rate. Additional studies are currently being planned to determine the seasonality of marine mammal mortality due to this fishery, and to assess future trends.

Miller *et al.* (1982) estimated that 10 sea-lions and as many as 30 pilot whales are

Table 7.3 The estimated marine mammal mortality in California fisheries for 1980 (data from Miller *et al.* 1982 and D. G. Ainley *et al.* personal communication).

Species	Fishery	Number
California sea-lions	commercial salmon trolling	300
	Klamath River gill-net	7[a]
	ocean gill-net + trammel-net	1209
	squid round-haul net	10
	anchovy-mackerel round haul	20
	trawl fishery	25
		1571
harbour seal	Klamath River gill-net	22[a]
	ocean gill-net	95
	in-shore gill-net	15[a]
		132
elephant seal	ocean gill-net	**25**
harbour porpoise	ocean gill-net	15
	in-shore gill-net	13[a]
		28
pilot whales	squid round-haul nets	30
	ocean gill-nets	30
		60
grey whale	ocean gill-net	**3**
baleen whale	ocean gill-net	**1**
total all fisheries		**1820**

[a] Actual count, total not estimated.

taken in the squid round-haul fishery in southern California (see Table 7.3). These estimates are based on limited information, as very few at-sea trips were made available by the fishermen. Sea-lions and pilot whales are shot at by fishermen in the squid dip-net fishery, but mortality is thought to be minimal.

In round-haul net fisheries for anchovy and mackerel, Miller *et al.* (1982) estimated that 20 California sea-lions were drowned per year. They also speculated that pilot whales may be taken in this fishery, but thought it likely that pilot whale mortality would be more common in the squid round-haul net fishery.

Finally, Miller *et al.* (1982) reported that a small number of sea-lions (see Table 7.3) are drowned by entering operating trawl nets; most have been drowned, but some lived and were returned to the water. Sea-lions are known to follow trawl nets and feed on smaller fishes passing through the webbing.

The impact of the incidental mortality presented in Table 7.3 is difficult to predict and will only be briefly discussed. Population estimates are only roughly known for some of the impacted species (Table 7.4). Relative to their maximum *per capita* growth rate, only the incidental take of California sea-lions and short-finned pilot whales is

Table 7.4 Estimated population size and percentage fishery-related mortality rate for marine mammals that occur off the coast of California.

Species	Population	Mortality from fisheries (%)	References
California sea-lion[a]	45 000–60 000	3–4	Le Boeuf and Bonnell (1980)
Pacific harbour seal			
Oregan border to Pt Conception	17 000		Miller *et al.* (1982)
Channel Islands	3 000	<1	Stewart and Yochem (1982)[1]
	20 000		
northern elephant seal	60 000–90 000	<1	Le Boeuf and Bonnell (1980)
harbour porpoise[b]			
short-finned pilot whales[b]	400–2 000	3–15	Dohl (1980), Stewart and Yochem (1982)
grey whale	16 000	<1	Reilly (1981)

[a] US population only.
[b] California population.

significant. More information on the population size of harbour porpoise is needed to determine the significance of the observed level of take. In all cases where incidental take occurs, the age and sex composition of the take is unknown.

Coastal marine mammal salvage programme

Additional information on marine mammal–fisheries interactions can be collected via salvage of beached marine mammals. In 1979, the Southwest Fisheries Center (SWFC) initiated a co-operative programme among San Diego area researchers to inspect and salvage stranded marine mammals from beaches in San Diego County. Dead marine mammals are recovered routinely in this programme by staff of the Coastal Marine Mammal Project, SWFC. In addition to collecting basic data (species, sex, morphometrics, photographs) from each stranding, the staff also thoroughly inspects each carcass for external wounds or trauma which might be human related. Carcasses which are judged not excessively decomposed (usually having been dead less than approximately 48 hours) are collected intact and subsequently undergo a thorough necropsy by a marine mammal veterinarian.

Events leading to traumatic death of marine mammals may, but will not always, result in a carcass exhibiting injuries, wounds, or other obvious signs of the cause of death. Gunshot wounds are usually readily detectable even in decayed carcasses. Because of firearm restrictions on virtually all beaches in San Diego County, shooting of already beached dead animals seldom occurs, hence any bullet wound is likely to have been incurred while the animal was alive. Cetaceans which are found with severed flukes and missing terminal vertebrae can generally be assumed to have been entangled in a net, though it is not evident whether these animals died as a direct result of the injury or suffocated in a net and were subsequently cut loose. Live, 'tailless' whales, both grey whales (*Eschrichtius robustus*) and short-finned pilot whales, have been observed in southern California. Suffocation resulting from entanglement in a net results in tissue damage which is difficult to detect, and evidence for suffocation is often circumstantial. The presence of gastric contents and vomitus in the oesophagus, and froth or foam in the trachea suggests suffocation. The presence of food in the stomach generally indicates some form of sudden, untimely death, as chronically ill marine mammals which strand generally have empty stomachs.

In 1980, 16% (3 of 19) of the recovered sea-lions showed evidence of human-related mortality; all four of the salvaged pilot whales showed evidence of fishery interactions. In 1981, 34 marine mammal specimens were fresh enough to autopsy; all but four of these were sea-lions. Gunshot wounds were the most common cause of death (37%). The next most frequent cause was hypoglycemia (18%; Hansen 1981). We hope that the data collected from this type of research will provide enough information to ascertain what proportion of the total mortality is due to human activities, including commercial and recreational fisheries.

Conclusion

A financial loss of approximately $600 000 per year was found to be related to marine mammal–fishery interactions in California. Over half of this loss was from salmon fisheries. This represents damage to the catch and to gear, and does not include losses due to frightening of fish from nets or from reducing the availability of target species. The incidental mortality of marine mammals is roughly 1800 animals per year. Though not known precisely, the *per capita* mortality rate due to fishery interactions is probably only significant for California sea-lions and short-finned pilot whales. Without information on stock discreteness and the age–sex composition of the take, it is not possible to determine the impact of fishery-related mortality on any of the populations involved. Because of problems relating to placing observers on commercial fishing boats, the age–sex composition of animals caught incidental to commercial fishery activities will have to be inferred from salvaged marine mammals. Studies directed at monitoring population trends of impacted species will have to be continued to ensure that this type of human activity does not adversely affect any of the stocks of marine mammals that occur off the coast of California. Studies directed at mediating losses to fishermen are currently underway by both the California Department of Fish and Game and the National Marine Fisheries Service.

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References

Ainley, D. G., D. Croll and T. Keating 1981. Personal communication from Point Reyes Bird Observatory, Bolinas, California and Moss Landing Research Laboratory, Moss Landing, California.

Dohl, T. P. 1980. Final contract report AA550-CT7-36, Vol. II. Univ. of California, Santa Cruz.

Hansen, 1981. Marine mammal salvage program report for 1981. *Admin. Rep.*

Herder, M. J. 1982. *Pinniped–fishery interactions in the Klamath River system, July 1979 to October 1980.* Final contract report, No. 79-ABC-00149.

Le Boeuf, B. J. and M. L. Bonnell 1980. Pinnipeds of the California Channel Islands: abundance and distribution. In *The California Islands: proceedings of a multidisciplinary symposium*, D. Powers (ed.), 175–96. Santa Barbara, Calif.: Santa Barbara Museum of Natural History.

Miller, D. J. 1981. *Marine mammal–fisheries interaction study.* Southwest Fisheries Center Administrative Report No. LJ-81-01C.

Miller, D. J., M. J. Herder and J. P. Scholl 1982. *California marine mammal–fishery interaction study, 1979–1981.* Final contract report, No. 79-ABC-00149.

Reilly, S. B. 1981. Population assessment and population dynamics of the California grey whale (*Eschrichtius robustus*). PhD dissertation, University of Washington.

Stewart, B. and P. Yochem 1982. Final contract report 82-ABA-02069, HSWRI Tech. Report 82-143. Hubbs/Sea World Research Institute.

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MILKFISH, *CHANOS CHANOS* (FORSSKÅL, 1775), TAKEN IN SOUTHERN CALIFORNIA ADDS NEW FAMILY (CHANIDAE) TO THE CALIFORNIA MARINE FAUNA

Six milkfish, *Chanos chanos,* taken in 1982 and 1983 establish the presence of the family Chanidae in California.

On 22 March 1982 fisherman Luigi San Filippo caught an unusual fish while gill netting for striped mullet, *Mugil cephalus,* with a 3½-inch mesh net, in the warm water discharge plume of a south San Diego Bay power plant (lat 32° 36′ 30″ N, long 117° 06′ 30″ W). One of us (JMD) was contacted and identified the fish as a 925 mm total length (TL), 680 mm standard length (SL), 5.6 kg, milkfish (Figure 1). The specimen is deposited at Scripps Institution of Oceanography, Division of Marine Vertebrates (SIO 82-22).

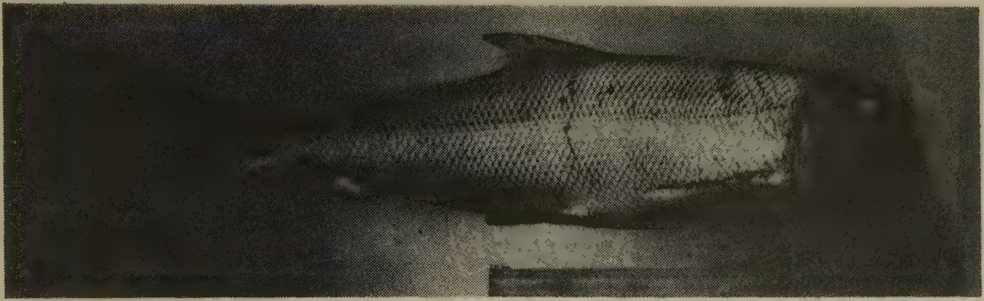

FIGURE 1. *Chanos chanos* taken by Luigi San Filippo in south San Diego Bay, March 22, 1982. Rule is 305 mm. *Photograph by John M. Duffy.*

Two other fishermen caught milkfish off the southern California coast in 1982 and one was taken in 1983. On 7 August 1982 a specimen was taken just outside the San Pedro breakwater (lat 33° 42′ 25″ N, long 118° 15′ 00″ W) by John Guglielmo in a gill net. The late John E. Fitch, California Department of Fish and Game, retired, identified the fish and determined its length to be 970 mm TL, 745 mm SL, and its weight to be 7.3 kg. It is deposited at the Natural History Museum of Los Angeles County (LACM 42887-1).

On 9 August 1982 three more milkfish were taken in the San Diego area. Fisherman Mike Irey caught them in a 6½-inch mesh gill net set in heavy kelp (*Macrocystis* sp.) off Point Loma, near the entrance to San Diego Bay (lat 32° 41′ 00″ N, long 117° 16′ 00″ W). Denyse Racine, California Department of Fish and Game, identified the fish, measuring 1024 mm TL, 1047 mm TL, and 1055 mm TL and weighing 7.9 kg, 9.3 kg, and 8.6 kg, respectively. All three fish were sold for food.

On 30 December 1983 Stephan Hadley snagged a milkfish with an artificial lure, in Quivira Basin, Mission Bay (lat 32° 45′ 45″ N, long 117° 14′ 15″ W). Sportsmen's Seafood Market retained the fish until Hannah Bernard and Bob Read, California Department of Fish and Game, identified the specimen as a 1010 mm TL, 765 mm SL, 7 kg, milkfish. Richard Rosenblatt, SIO, examined the fish and determined that it was a mature female with inactive oocytes. The fish is deposited at SIO (SIO 83-177).

Schuster (1960) reported the world wide range of *C. chanos* to include the tropic and subtropic sections of the Indian and Pacific Oceans, 30° to 40° N to 30° to 40° S lat and 40° E to 100° W long. Neither Miller and Lea (1972) nor Hubbs, Follett, and Dempster (1979) included its range along the California coast. Fowler (1938) added the Galapagos Islands and Chirichigno (1978) the coast of Peru for recent uncommon records of *C. chanos;* yet the milkfish is not uncommon in the Gulf of California from Guaymas to Mazatlan (Evermann and Jenkins 1981, Jordan 1895, Thomson and McKibbin 1976). Migdalski and Fichter (1976) suggest the possible presence of *C. chanos* along the coast of "lower California," which we infer from historical usage to mean Baja California, Mexico. Eschmeyer, Herald, and Hammann (1983, p. 63) note that the milkfish "occasionally strays to S. Calif."; this information was provided by the late John E. Fitch (William N. Eschmeyer, California Academy of Sciences, pers. commun.).

In 1877, 100 milkfish were brought to California from Hawaii in exchange for salmon and trout eggs (Calif. Comm. of Fisheries 1877). The fish were introduced in a small stream at Bridgeport, Solano County. There is no record of their survival.

There have been, however, three reports of the milkfishes' appearance along the coast of Baja and southern California during the last 55 years. Clark (1929) reported a specimen in a San Pedro fish market that had been taken "off the western coast of Lower California." A milkfish was observed floating dead in south San Diego Bay, also in 1929 (John E. Fitch, pers. commun.). Not until May 1979 was another specimen noted. San Diego fisherman Ed Simpson caught a milkfish on hook-and-line in south San Diego Bay, near where San Filippo's fish was taken. Richard Rosenblatt, SIO, identified the specimen as a milkfish from the remains of the caudal peduncle and caudal fin which are deposited at SIO (SIO 79-345).

The 1982 specimen from off San Pedro represents a northern range extension of approximately 1786 km from an area off the west coast of Mexico between Mazatlan and Guaymas (Figure 2). We believe that this locale is the most likely source for these fish. Our specimens were all large and presumably adult fish (maximum reported size 1.7 m—in Nelson 1976) which would easily be able to make the journey to our coastline.

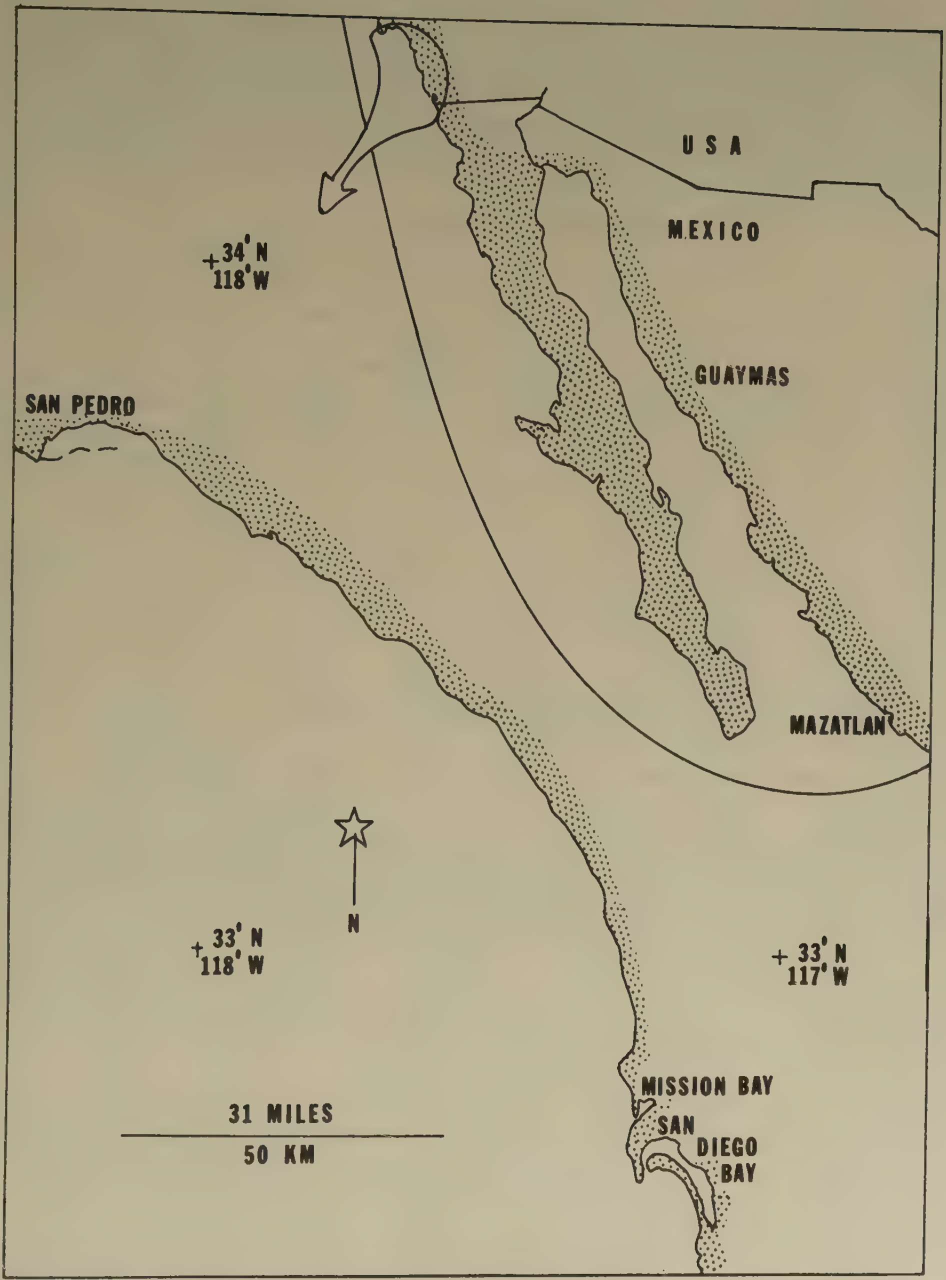
U S A
MEXICO
GUAYMAS
MAZATLAN
34° N 118° W
SAN PEDRO
N
33° N 118° W
33° N 117° W
MISSION BAY
SAN DIEGO BAY
31 MILES
50 KM

FIGURE 2. *Chanos chanos* catch locations in southern California. Inset is not to scale.

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Hadley's fish. R. N. Lea and H. W. Frey both provided references, reviewed the manuscript, and provided helpful comments. G. Quiros checked all literature citations. The late J. E. Fitch provided measurements of the San Pedro specimen and references, observations, and encouragement unobtainable from any other source. D. Gittings, National Marine Fisheries Service and P. Leverenz, SIO, provided assistance in obtaining references.

LITERATURE CITED

California Commissioners of Fisheries. 1877. Report of the Commissioners of Fisheries of the State of California for the years 1876 and 1877. 30 p.

Chirichigno F. N. 1978. Nuevas adiciones a la ictiofauna marina del Peru. Inst. del Mar del Peru Informe No. 46. 109 p.

Clark, F. N. 1929. Specimen of milkfish, *Chanos chanos,* delivered at San Pedro. Calif. Fish Game 15(2):175.

Eschmeyer, W. N., E. S. Herald, and H. Hammann. 1983. A field guide to Pacific coast fishes of North America. Houghton Mifflin Co., Boston. 336 p.

Evermann, B. W., and O. P. Jenkins. 1891. Fishes from Guaymas. Proc. U.S. Natl. Mus. 14 (846):121–165.

Fowler, H. W. 1938. The fishes of the George Vanderbilt South Pacific Expedition, 1937. Monog. Acad. Nat. Sci. Phila. 2:1–349.

Hubbs, C. L., W. I. Follett, and L. J. Dempster. 1979. List of the fishes of California. Occas. Pap. Calif. Acad. Sci., No. 133:1–51.

Jordan, D. S. 1895. The fishes of Sinaloa. Proc. Calif. Acad. Sci., 5 (ser. 2):377–514.

Migdalski, E. C., and G. S. Fichter. 1976. The fresh & salt water fishes of the world. Alfred A. Knopf, Inc., New York. 316 p.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. Fish Game, Fish Bull. 157:1–235.

Nelson, J. S. 1976. Fishes of the world. John Wiley and Sons, Inc., New York. 416 p.

Schuster, W. H. 1960. Synopsis of biological data on milkfish, *Chanos chanos* (Forskål), 1775. FAO Fish. Biol. Synop. 4:1–58.

Thomson, D. A., and N. McKibbin. 1976. Gulf of California fishwatcher's guide. Golden Puffer Press, Tucson, Ariz. 75 p.

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Fisheries Applications of Satellite Data in the Eastern North Pacific

PAUL C. FIEDLER, GARY B. SMITH, and R. MICHAEL LAURS

ABSTRACT—Satellite sensors provide extensive and detailed images of sea surface temperature and color. Synoptic daily sampling by satellites gives a unique view of the ocean surface that can be extremely useful when used in conjunction with conventional shipboard data. Current and potential applications of satellite data off the U.S. Pacific coast and Alaska include interpretation of ship survey data, explanation of pelagic fisheries distributions, prediction of stock recruitment, spatial/temporal monitoring of the coastal zone and sea ice, studies of migration routes and timing, and production of charts to aid commercial fisheries.

Introduction

Remote sensing of the ocean is playing an increasingly important role in fishery research and fish harvesting along the Pacific coast of the United States and Canada. Satellite sensors make synoptic measurements of water temperature and color, winds, ice cover, wave height, and surface currents over large areas of the ocean surface. Variations in these ocean conditions play key roles in natural fluctuations of fish stocks and in their vulnerability to harvesting.

The promise of remote sensing techniques for fisheries research, management, and exploitation has been recognized since the early 1960's when the first visible and infrared images of the earth's surface were obtained from orbit. However, successful applications have only recently been realized with the advent of advanced and sensitive radiometers, high-speed data processing, and the availability of imagery to fishery scientists and fishermen.

Gower (1982) provides a useful overview of the different kinds of remote sensing data relevant to fisheries science and oceanography. Laurs and Brucks (In press) review living marine resources applications in the United States. Yamanaka (1982) gives examples of some uses of satellite data for fisheries applications off Japan. Other potential, ocean-related uses of remote sensing data were discussed by Montgomery (1981). This paper will review the satellite sensors currently measuring sea surface temperature and ocean color, data processing and availability, and several examples of recent and potential applications to eastern North Pacific fisheries.

Satellites provide a unique view of the ocean by covering large areas synoptically. Coverage of historically data-poor areas is particularly useful. However, satellite measurements are usually limited to the surface or near-surface layers in cloud-free areas. Therefore, satellite data complement conventional shipboard observations but cannot replace them. The best research approach often requires close coordination of the two sources of information. In this way, the evolving capabilities of satellite remote sensing are providing a powerful tool to enhance the efficient use of living marine resources.

Satellite Sensors

A variety of instruments measure radiance from the earth's surface in visible, thermal infrared (IR), and microwave wavelength bands (Table 1). The most readily available and useful data come from the Advanced Very High Resolution Radiometer (AVHRR) on meteorological satellites operated by the National Oceanic and Atmospheric Administration (NOAA) and the Coastal Zone Color Scanner (CZCS) on the experimental Nimbus-7 satellite operated by the National Aeronautics and Space Administration (NASA). These advanced sensors are characterized by high sensitivity in narrow wavelength bands, fine ground resolution, and extensive data archival.

Satellites receive electromagnetic radiation emitted from the sea surface (the IR temperature signal) and back scattered from below the surface (the visible ocean color signal). These signals are contaminated by reflection from the sea surface and clouds, and by absorption, emission, and scatter by atmospheric particulates and molecules. Some of these errors can be eliminated or minimized very simply. For example, sunglint and "limb darkening" (by long atmosphere paths at oblique viewing angles) are avoided by constraining the viewing geometry of the sensor. Corrections of some other errors, however, require advanced image processing methods.

Dense clouds may so completely absorb visible and IR radiation from the sea surface that no type of data

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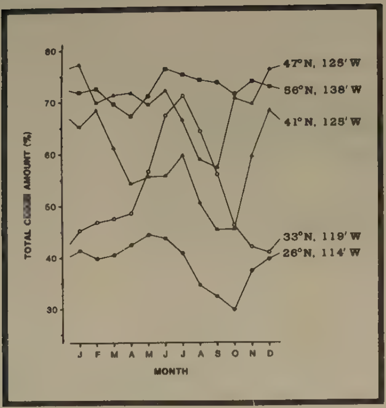

Figure 1.—Mean monthly total cloud amount over coastal waters, from surface marine weather observations, 1921-72 (Nelson and Husby, 1983): Baja California (27°N, 115°W), Southern California Bight (33°N, 119°W), Cape Mendocino (41°N, 125°W), Vancouver Island (48°N, 126°W). Gulf of Alaska data (56°N, 138°W) are from satellite observations, 1967-72 (Sadler et al., 1976), intercalibrated against data from Nelson and Husby (1983).

Table 1.—Some satellite sensors measuring visible, infrared, or microwave radiance for oceanographic measurements. Wavelengths are band midpoints. Ground resolution dimensions are directly beneath the satellite.

Sensor[1]	Satellite	Channel	Spectral band	Wavelength (μm)	Scan width (km)	Ground resolution (km)	Primary measurements
AVHRR	TIROS-N NOAA-6, 7, 8	1	Visible	0.63	3,000	1.1	Sea surface temperature, sea ice
		2	Near-infrared	0.91			
		3	Infrared	3.74			
		4	Infrared	10.8			
		[2]5	Infrared	[2]12.0			
CZCS	Nimbus-7	1	Visible	0.44	1,566	0.825	Phytoplankton pigments, turbidity, sea surface temperature
		2	Visible	0.52			
		3	Visible	0.55			
		4	Visible	0.67			
		5	Near-infrared	0.75			
		6	Infrared	11.5			
MSS	LANDSAT	1	Visible	0.55	185	0.079	Water color, turbidity, sea ice
		2	Visible	0.65			
		3	Near-infrared	0.75			
		4	Near-infrared	0.95			
VISSR	GOES	1	Visible	0.62	Earth disk	7×3	Cloud cover, sea surface temperature
		2	Infrared	11.5			
SMMR	Nimbus-7 SEASAT	1	Microwave	4.54×10^4	600	20-100	Sea surface temperature, sea ice, near-surface winds
		2	Microwave	2.8×10^4			
		3	Microwave	1.66×10^4			
		4	Microwave	1.36×10^4			
		5	Microwave	0.81×10^4			

[1] Sensors: AVHRR = Advanced Very High Resolution Radiometer; CZCS = Coastal Zone Color Scanner; MSS = Multispectral Scanner; VISSR = Visible and Infrared Spin Scan Radiometer; SMMR = Scanning Multichannel Microwave Radiometer.

[2] Channel 5 on NOAA-7 and NOAA-8 satellites only.

processing can retrieve a useful signal. Clouds severely limit satellite coverage of the sea surface in some regions of the eastern North Pacific, particularly north of lat. 40°N (Fig. 1). South of lat. 27°N, off Baja California, mean monthly cloud cover is consistently less than 50 percent, due to persistent offshore flow of dry continental air. From lat. 30°N to 38°N, coastal waters are covered by a dense layer of low stratus clouds during the summer upwelling season (Nelson and Husby, 1983). The most favorable conditions for remote sensing at these latitudes are found from October through March or April, especially during occasional brief periods when Santa Ana winds blow warm, dry desert air offshore and produce cloud-free conditions up to 1,000 km from the coast.

In contrast, the most cloud-free conditions at lat. 40°–50°N are found in late summer, from August to October. Mean monthly cloud cover increases to the north and is consistently 70 percent or greater in the Gulf of Alaska, although March and April may be relatively clear. As a general rule, percent cloud cover increases by at least 10 percent from the coast to a distance on the order of 200 km offshore in the eastern North Pacific (Nelson and Husby, 1983).

The probability of cloud-free conditions in a region of interest during regular satellite passes is loosely reflected in these monthly cloud cover statistics. Cloud cover restricts the extent to which satellite data can be anticipated, or depended upon, to be available. Whereas it may be possible to obtain regular daily or weekly coverage of sea surface features in the south, such as in the Southern California Bight, in the north there are generally more frequent and longer data gaps. Satellite coverage of ocean features in the Alaska region is characteristically limited to occasional cloud-free scenes that, despite being infrequent, can be rich in information. Microwave radiometers can measure sea surface temperature through clouds, but with a lower sensitivity and much coarser resolution than IR radiometers.

Data Processing

The AVHRR measures thermal infrared radiant energy in three wavelength bands (Table 1). Temperature calibration data are obtained by scanning deep space and internal blackbody targets. Accurate sea surface temperatures are calculated from empirical regressions of ship and buoy temperatures on satellite temperatures in two or three bands. Such multispectral corrections are based on the different response of each band to the cold bias caused by atmospheric water vapor (McClain et al., 1983). Pixels (samples) containing clouds even smaller than the sensor's field of view are screened in daytime passes using the near-infrared albedo data from channel 2 (Bernstein, 1982).

The CZCS measures visible light in five narrow wavelength bands selected for estimating phytoplankton pigments, suspended sediments, and dissolved organic matter. Up to 90 percent of the visible radiance received at the satellite is skylight reflected and scattered within the atmosphere. Corrections are based on assumptions that the red light emitted by the ocean and measured by channel 4 is either negligible or can be accurately predicted from radiances in other bands. The atmospheric radiance measured by channel 4 can then be related to atmospheric radiances in other channels using known spectral properties of atmospheric scattering (Gordon et al., 1983). Corrected ratios of blue to yellow-green (channel 1/channel 3) or green to yellow-green (channel 2/channel 3) radiance are then used to calculate phytoplankton pigment concentration from empirical regression relationships (Smith and Baker, 1982).

Satellite data, properly corrected for the various errors described above, have been validated by sea truth data from ships to ± <1°C (Bernstein, 1982) and ±0.4 log chlorophyll concentration (Smith and Baker, 1982). While important subsurface features such as chlorophyll maximum layers and some cold-core eddies or oceanic fronts may not be detected by satellites, the measured parameters are, in general, closely related to properties such as mixed-layer temperature and integrated chlorophyll or primary productivity in the euphotic zone (Smith, 1981).

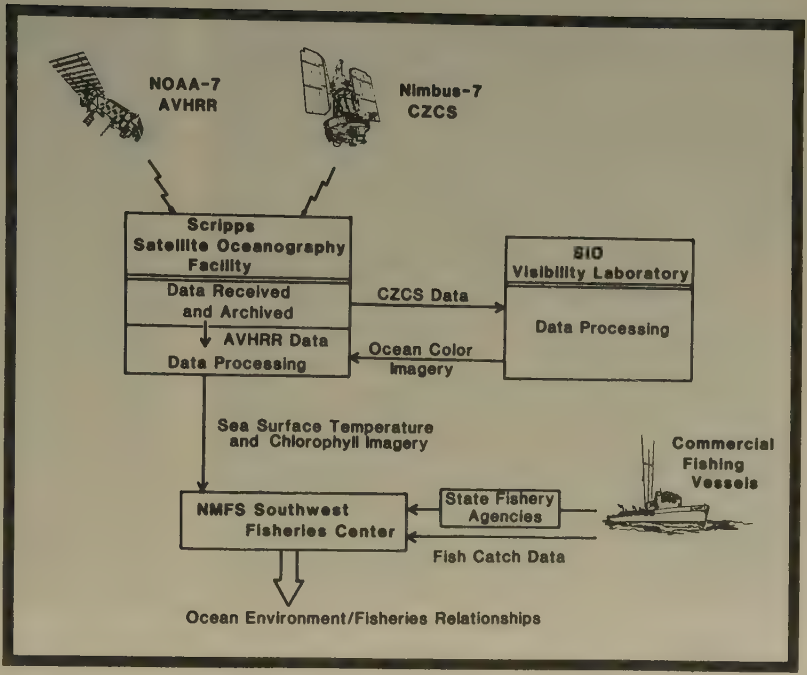

Figure 2.—Satellite data collection and processing network utilized by the National Marine Fisheries Service on the west coast.

Data Availability

Applications of satellite data are ultimately limited by their availability. Ideally, a user would have immediate access to data received directly from satellites and conveniently archived, with data processing facilities at his fingertips. This ideal has been approached by an arrangement at the Satellite Oceanography Facility of Scripps Institution of Oceanography in La Jolla, Calif., for most of the work reported here (Fig. 2). Similar arrangements, lacking direct data reception capabilities, have been established at the University of Miami and by the Northeast Area Remote Sensing System, which is a regional association of university, industry, and government organizations that was recently formed in the northeastern United States.

Global satellite data are archived by the Satellite Data Services Division of NOAA and are available to the public, although acquisition may require several months and a large backlog of CZCS data is unprocessed. AVHRR and CZCS data are available in various forms including photographic prints and negatives, digital data on magnetic tapes, and maps of derived sea surface temperature and ice cover. These products and a catalog of available CZCS data are available from the National Environmental Satellite Data and Information Service, Satellite Data Services Division, NOAA, Room 100, World Weather Building, Washington, DC 20233. Detailed procedures for obtaining environmental satellite data are given in Cornillon[1]. In general, photographic copies of raw data are of limited value and a user must have access to a computer-based, image processing system to extract useful information from satellite data on digital tapes (this situation may change in the future if products derived from satellite data are offered by commercial processing enterprises).

Applications

We briefly review here examples of general applications of satellite data to fisheries research and management problems along the Pacific coast between California and Alaska. Some of these examples have been published elsewhere, but none of the applications has as yet been fully realized.

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[1] Cornillon, P. 1982. A guide to environmental satellite data. Univ. R. I. Mar. Tech. Rep. 79, 469 p. Available for $20.00 from the University of Rhode Island, Marine Advisory Service, Publication Unit, Narragansett, RI 02882.

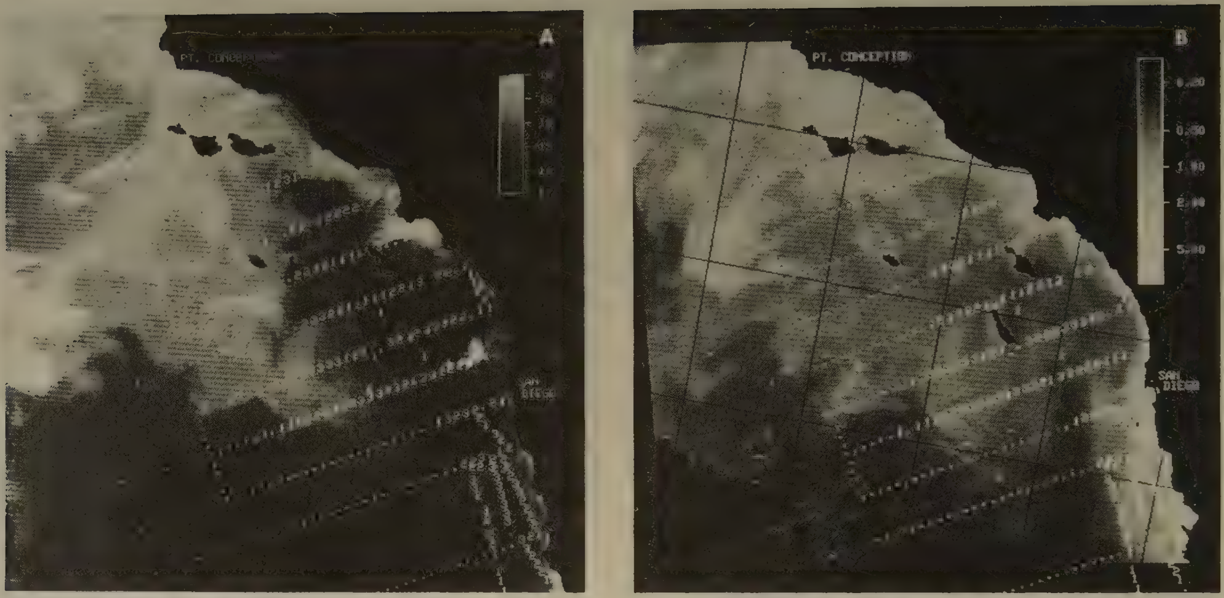

Figure 3.—Northern anchovy egg distribution, 20 March-10 April 1980; • = 0, 1 = 1-4, 2 = 5-17, 3 = 18-245 eggs/0.05 m². Top photo (A) is sea surface temperature (°C) from NOAA-6 AVHRR, 7 April 1980; Photo B is of phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, 8 April 1980.

Interpretation of Ship Survey Data

A large stock of northern anchovy, *Engraulis mordax,* is found off southern California, where intensive egg surveys have been conducted since 1980 to estimate spawning biomass. Satellite images of sea surface temperature and phytoplankton pigment concentration, obtained during an egg survey in April 1980, depict environmental limits on the range of spawning anchovy (Fig. 3). North of San Diego, no eggs were found in water colder than 14°C. To the south, spawning northern anchovy were confined along the coast to a narrow band of water with high pigment concentrations. Similar distribution patterns were observed in 1981 and 1982 (Lasker et al., 1981; Fiedler, 1983).

The distribution of spawning adults may reflect the critical need by first-feeding larvae for aggregations of suitable food organisms in a stable water column. The environmental limits revealed by the satellite images would not have been revealed by the egg survey data alone, because phytoplankton pigments were not measured and spatial coverage was limited.

Satellites data may be used to interpret the large-scale patterns and possible causes of spatial/temporal variability in other types of ship survey data. Most measurements of fish eggs and larvae, plankton concentrations, chlorophyll, nutrients, temperature, and salinity are made at point locations at regular intervals along transects or in grid patterns. Remote sensing data collected concurrently, if available, may provide valuable information on factors contributing to patterns in the shipboard data and on conditions beyond the area surveyed. Besides the insight that usually results from a synoptic view, this information is important in evaluating the validity of interpolation and extrapolation of ship survey results.

Pelagic Fisheries Distribution

Albacore, *Thunnus alalunga*, is a migratory oceanic tuna that is an important target species for jigfishing, live bait, and recreational fishing along the U.S. Pacific coast from July to October. Fishermen search for aggregations of these fish in warm, blue oceanic waters near temperature or water color fronts at the offshore edge of productive coastal waters. Daily catch records during peak fishing in late summer 1981 were taken from logbooks submitted to west coast state fisheries agencies. Concentrations of fishing activity and large catches indicate sites of albacore aggregations.

Satellite images of sea surface temperature and phytoplankton pigment concentrations clearly show favorable sites for aggregations in pockets of warm, blue oceanic water intruding into the colder and more turbid coastal water mass (Fig. 4; Laurs et al., In press). Albacore are visual predators and may feed most efficiently in the clear water adjacent to coastal waters where prey densities are higher. Albacore fishermen, running several days out of port in small boats to reach offshore fishing grounds, can benefit from timely maps of sea surface temperature and ocean color gradients derived from satellite data. Potential benefits include decreased search time, lower fuel use, and increased catches.

Satellite data may be applied to

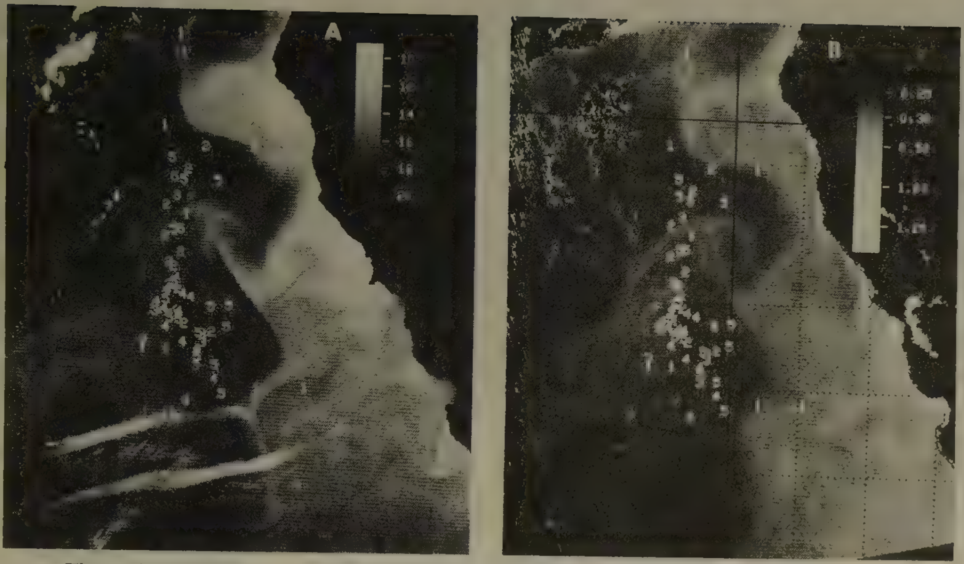

Figure 4.—Daily albacore catches off central California, 19-24 September 1981: 1 = 0-27, 2 = 33-63, 3 = 64-81, 4 = 87-140, 5 = 148-750 fish/boat. A is sea surface temperature (°C) from NOAA-7 AVHRR, 21 September 1981; B is phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, 22 September 1981.

other pelagic fisheries, both to direct fishing effort and for fisheries management. In the Pacific Northwest and off Alaska, five species of Pacific salmon—sockeye salmon, *Oncorhynchus nerka*; chum salmon, *O. keta;* pink salmon, *O. gorbuscha*; chinook salmon, *O. tshawytscha*; and coho salmon, *O. kisutch*—are important resources for a large fishing industry. During their oceanic life history phase, these salmon are caught by power or hand-trolling boats using methods similar to albacore fishing. The study described by Borstad et al. (1982) is an example of a use of remote sensing techniques to study relationships between salmon distributions, fishing, and oceanographic conditions. Other pelagic resources for which there may be analogous applications include Pacific herring, *Clupea harengus pallasi,* off Alaska; jack mackerel, *Trachurus symmetricus,* and Pacific mackerel, *Scomber japonicus,* off California; and bluefin tuna, *Thunnus thynnus orientalis,* off Baja California.

Stock Recruitment Predictions

An application of satellite data that merits investigation is the improved understanding and prediction of variations in recruitment to coastal fish stocks. In the eastern North Pacific, offshore transport and turbulent mixing may have important effects on the larval survival and subsequent recruitment of some species (Bakun and Parrish, 1982). Both processes are driven by surface wind stress. Offshore transport removes eggs and larvae from productive nearshore nursery grounds. This may be most important where strong seasonal upwelling occurs over a narrow continental shelf, as it does along the U.S. coast north of lat. 34°N. Turbulent mixing reduces stratification of the near-surface water column and disrupts aggregations of food organisms required for successful first feeding by newly hatched larvae (Lasker, 1981).

Variations in annual recruitment of Pacific whiting, *Merluccius productus,* have been related to monthly mean Ekman transport estimated from equatorward wind stress off central California (Bailey, 1981). Fiedler (1984) has used AVHRR imagery to document interannual changes in the sea surface temperature field related to variations in coastal upwelling off the U.S. Pacific coast. Satellite imagery has also revealed that offshore transport is a highly irregular process in both time and space, manifested as meandering jets and eddies of cold water (e.g. Fig. 5). Offshore transport could perhaps be quantified by measuring the areal extent of relatively cold water nearshore or the offshore displacement of frontal features between daily satellite passes. This application may be extended to other species for which there is evidence of similar environmental effects (e.g. Hayman and Tyler, 1980; Bakun and Parrish, 1982).

The seasonal timing and spatial location of northern anchovy spawning has been related to turbulent mixing, as indexed by the cube of mean surface wind speed in historical marine weather observations, by Husby and Nelson (1982). They suggested that strong year classes may depend upon the occurrence of "time-space windows" with sufficiently low turbulence to allow development of layers of food organisms.

The magnitude and direction of surface wind stress are directly

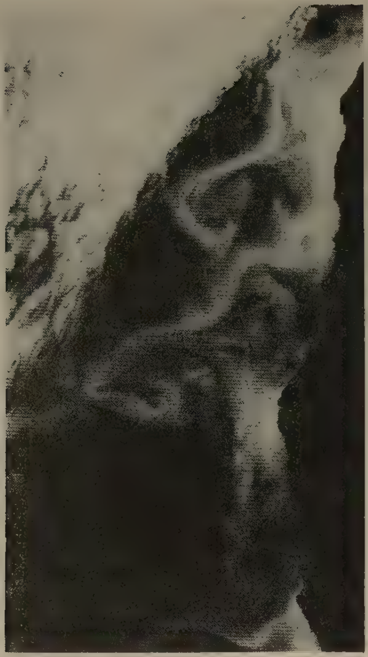

Figure 5.—Localized offshore transport of cold upwelled water (whiter shades) off northern California and southern Oregon. The three major coastal landforms, from top to bottom, are Cape Blanco, Cape Mendocino, and Point Arena. White features in the top left corner are clouds. Image from NOAA-7 AVHRR channel 4, 14 June 1982.

measurable by microwave sensors such as the scatterometer which flew on the short-lived SEASAT satellite in 1978. The U.S. government has not yet committed funds to orbit another such sensor, for which there are many potential scientific and commercial applications (NASA Satellite Wind Stress Working Group, 1982). Fisheries applications might include the real-time planning of fishing operations to avoid adverse sea state conditions, as well as the measurement of surface winds driving environmental processes affecting recruitment into coastal fish stocks. These benefits would be particularly significant in northern areas, such as the Pacific Northwest and Alaska regions, where present remote sensing coverage by visible and infrared sensors is usually limited by cloud cover.

Coastal Zone Monitoring

Mesoscale processes, such as upwelling and eddy formation, are very important components of the spatial and temporal variability of eastern North Pacific coastal waters, especially in the complex California Current System. Extensive and high-resolution satellite data are particularly valuable for studies of these processes (Bernstein et al., 1977). Anomalous ocean conditions along the U.S. Pacific coast were monitored during the 1982-83 El Niño event using AVHRR and CZCS data (Fiedler, 1984). Localized sea surface temperature anomalies up to +6°C were observed. Reduced coastal upwelling during the first half of the year was detected in patterns of cold, nearshore surface waters. CZCS images of the Southern California Bight indicated reduced phytoplankton productivity. This event affected many commercial and sport fisheries along the coast (Anonymous, 1984).

Monitoring coastal zone variability within a year or season with satellite data may be useful for developing better release strategies for hatchery-reared juvenile salmonids by enabling management decisions to be more adaptive and based on conditions in nearshore nursery areas. It might be possible to improve the growth and survival of hatchery-reared salmon by scheduling releases during periods of most favorable ocean conditions. AVHRR and CZCS imagery could be used as sources of information on sea surface temperature, river plume trajectory, upwelling intensity, primary production, and the oceanic frontal areas associated with each of these factors. Small improvements in the survival of juveniles released from hatcheries could result in substantial increases in the numbers of returning adults. If successful, this application would be particularly important in the Pacific Northwest and Alaska region, where hatchery operations are extensive and salmon resources have high value.

Salmon enhancement programs on the Columbia River, the largest river on the Pacific Coast of North America, provide an example of the potential. The National Marine Fisheries Service funds 22 salmon hatcheries and 7 rearing ponds on the Columbia River at an annual cost exceeding $4.5 million. Each year, these facilities culture and release 80-100 million salmon smolts in late April and early May. The present release schedule is decided largely on the basis of administrative criteria, tradition, and attempts to emulate nature. However, survival rates for these hatchery-reared salmon are relatively low, only about 3.7 percent (range, 0.23 to 12.35 percent) for coho salmon in their first year (Mathews, 1980).

There is increasing evidence that juvenile salmon survival, and subsequent adult returns, are critically influenced by conditions in the ocean environment within the first 6 months after hatchery release (Hartt, 1980; Wahle and Zaugg, 1982). Important factors may be food availability and the extent that food limitations occur in the nursery habitats as a result of crowding. On the Columbia River, although hatchery-reared salmon pass downstream and through the lower river and estuary relatively rapidly, significant losses occur in each of these migratory stages and areas. After reaching the ocean, juvenile salmon typically migrate along a relatively narrow coastal belt (Hartt, 1980). In purse seine studies off the Columbia River, juvenile salmonids (<50 cm) have been found to be distributed mainly within 28 km of shore; chinook salmon and steelhead, *Salmo gairdneri*, were distributed almost entirely in the river plume (Miller et al., 1983). Upwelling and its effects on food production have been related to juvenile survival and adult salmon production (Gunsolus[2]). A better understanding of these environmental relationships is a goal of current research.

Figure 6 shows three satellite images of sea surface temperatures along the Pacific Northwest coast during summer 1982, illustrating changes in coastal conditions that can occur over relatively short (2-3 week) time intervals. On 5 July, coastal upwelling was very weak, although signs of intensification were developing at Cape Mendocino. By 23 July, upwelling had intensified considerably, especially to the north. By 18 August, however, upwelling was again weaker. Changes in the mesoscale pattern of cold-water jets and meanders can be seen. In the latter two images, the Columbia River plume is indicated by a dark, warm-water break in the band of cold, upwelled water along the coast.

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[2] Gunsolus, R. T. 1978. The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery-reared stocks. Oreg. Dep. Fish Wildl., Columbia Reg. Off., 17330 S.E. Evelyn St., Clackamas, OR 97015. Unpubl. manuscr., 59 p.

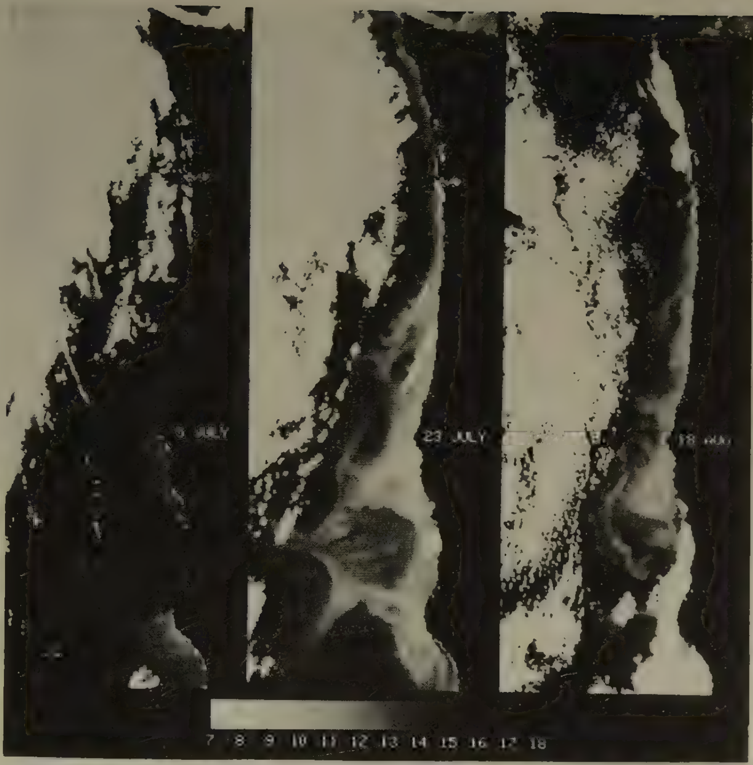

Figure 6. — Variations in the intensity and pattern of coastal upwelling off the Pacific Northwest between lat. 39°00′N and 48°30′N, July-August 1982. Sea surface temperature (°C) from NOAA-7 AVHRR channels 4 and 5. Clouds (white) screened with channel 2 data.

Monitoring Sea Ice

Sea ice is an important seasonal feature of the Alaskan environment that can be monitored by satellite coverage (Weeks, 1981; McNutt, 1981). Ice affects commercial fishing activities by threatening vessel safety, limiting navigation and access, and damaging fishing gear. Yet sometimes waters near the edge of pack ice can offer shelter or rich fishing grounds. Ice is also important because of its significance in the ecology of, and as a habitat for, northern marine mammals.

In the eastern North Pacific, winter ice cover occurs in inlets along the coasts of southeastern Alaska, the Gulf of Alaska, and the Aleutian Islands. Its formation is often associated with freshwater runoff, such as in Cook Inlet (Poole and Hufford, 1982). Freshwater ice forms on stream and river deltas, then sea ice forms in lower parts of the embayments. However, much greater ice cover occurs in the extended area to the north. Ice covers the Chukchi Sea, Bering Strait, and nearly the entire northeast half of the eastern Bering Sea during winter and spring. Movements of pack ice in the Bering Sea are influenced by winds and water currents, and are highly dynamic.

Ice off the North Slope, along the southern coast of Alaska, and in the Bering Sea, is monitored routinely by the National Weather Service. When cloud cover permits, ice and open water can be discriminated with a 1 km resolution using AVHRR visible and infrared data (Fig. 7). Combined with data from the Nimbus-7 Scanning Multichannel Microwave Radiometer, which are not influenced by clouds but have a resolution of 60 km, large-scale maps of ice coverage or concentration are produced. Some information about ice type (age and thickness) can be gleaned from satellite data, but the analysis is supplemented by aerial reconnaissance and reports from ships and shore stations. Ice analysis maps are distributed to users in the fishing and oil industries three times a week by radio facsimile and once a week by mail.

Winter fisheries affected by ice cover in the eastern Bering Sea include: Foreign groundfish fisheries, involving 200-300 vessels per year and an annual catch of about 1.3 million metric tons (Bakkala et al., 1979); highly-valued U.S. fisheries for king crab, *Paralithodes* spp., and snow (Tanner) crab, *Chionoecetes* spp. (Otto, 1981); and U.S. fisheries for Pacific herring that take place along the north shore of Bristol Bay. Vessels operating in these fisheries often need to work around sea ice, can have stability problems, and are sometimes trapped in shifting pack ice and lost.

Ice is an important part of the habitat of 25 species of marine mammals that occur in the Bering Sea (Fay, 1974; Burns et al., 1981). It may serve as a substrate, barrier, or to force migrations. Species that regularly come in contact with ice include the following: Polar bear, *Ursus maritimus;* walrus, *Odobenus rosmarus;* harbor seal, *Phoca vitulina;* ringed seal, *P. hispida;* ribbon seal, *P. fasciata;* bearded seal, *Erignathus barbatus;* narwhal, *Monodon monoceros;* beluga whale, *Delphinapterus leucas;* and bowhead whale, *Balaena mysticetus.* For these and other species, the wide views of ice

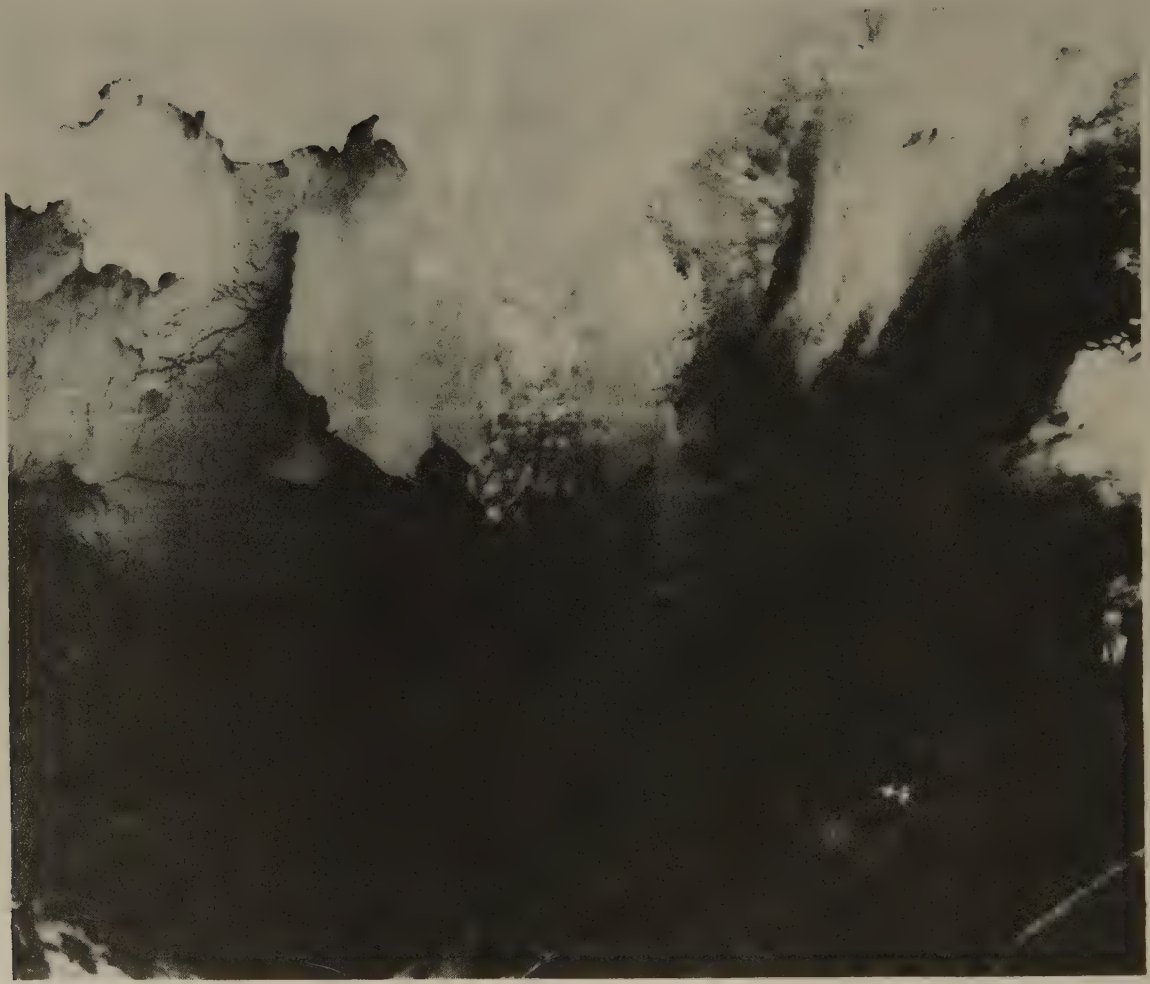

Figure 7.—Ice cover in the eastern Bering Sea, 18 February 1983, NOAA-7 AVHRR channel 4. Ice, clouds, and snow-covered land all appear whiter (colder) than open water. Pack ice extends from the Bering Strait, in the top left corner, past St. Matthew and Nunivak Islands, but does not reach the Alaska Peninsula to the southeast. Photograph courtesy of G. L. Hufford, NOAA/NESDIS, Satellite Field Services Station, Anchorage, Alaska.

characteristics that can be obtained from satellite imagery provide unique information for use in conservation and management.

Migration Routes and Timing

Satellite imagery can provide useful information on environmental conditions related to the routes and timing of long-distance migrations by marine mammals and fish. In the eastern North Pacific and in waters off Alaska, many important species occupy large habitat areas and make extensive seasonal migrations. These large activity areas are often in remote and data-poor regions. Satellite coverage, because of its wide areal views and long-term repeated observations, provides data with time and space characteristics that are appropriate for interpreting large-scale migratory phenomena. Applications include planning research, experimental design, and evaluating strategies for population enumeration.

The North Pacific albacore, *Thunnus alalunga,* performs transpacific migrations and supports important commercial fisheries in the western, central, and eastern North Pacific. Seasonal migration into North American coastal waters is associated with the Transition Zone between Pacific central and subarctic water masses (Laurs and Lynn, 1977). The frontal structure of these waters may affect both the timing and location of the arrival of albacore into the summer fishery along the coast. Figure 8 illustrates CZCS color frontal patterns in the central Pacific that could influence the course of the migration.

The potential for using both color and infrared temperature imagery in

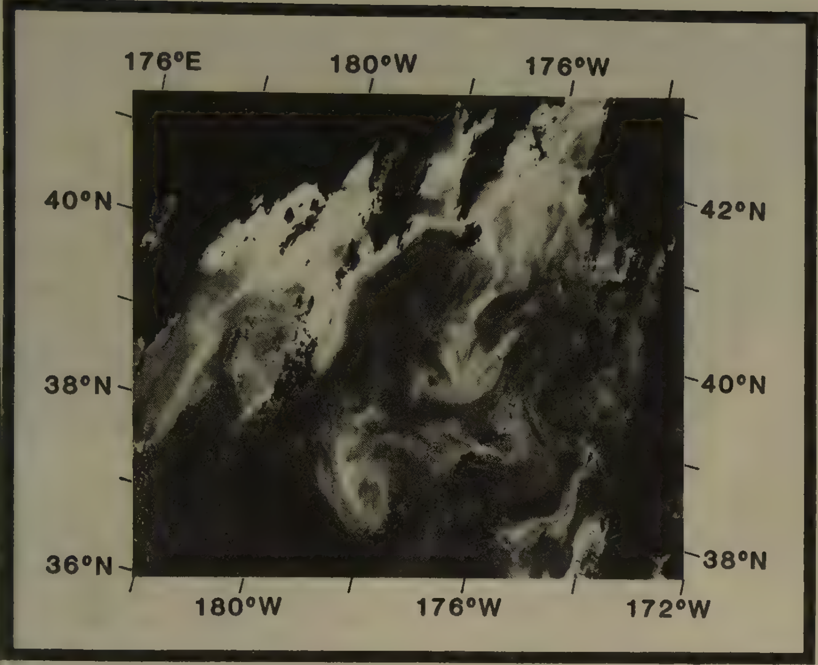

Figure 8.—Phytoplankton pigment concentration in a 600 × 600 km area of the central North Pacific, measured by the Coastal Zone Color Scanner, 30 June 1980. Black = clouds, darkest gray = 0.08 mg m^{-3}, white = 5.7 mg m^{-3}.

ishery operations in these waters has been explored on a limited basis with promising results. Although cloud cover allows only infrequent views of the sea surface, the surface patterns seem to be less dynamic than in coastal waters. Color boundaries are detectable from satellites during all seasons, but pronounced sea surface temperature fronts are not present during summer-autumn due to seasonal warming. However, infrared satellite imagery has been used to locate the subtropical front during winter (Van Woert, 1982) and spring months[3].

In Arctic and subarctic areas, such as the Beaufort Sea and northern Bering Sea, the movements and distribution of sea ice have important influences on the movements of marine mammals. Bowhead and beluga whales make regular seasonal migrations through the shear zones and lead systems that develop in the Arctic pack ice (Braham et al., 1980). In the case of the bowhead whale, the prediction and evaluation of migration paths is important because it is an endangered species and the western Arctic population requires careful annual censusing. Satellite imagery showing ice cover and open-water corridors is used to spot check the sampling design for summer whale counts.

There is potential for similar applications of satellite data in other oceanic and coastal areas, although the relationships between environmental characteristics and marine mammal migrations are not as obvious. For example, the eastern Pacific stock of gray whale, *Eschrichtius robustus*, undergos regular annual migration between summer feeding grounds in the Chukchi Sea and winter breeding grounds in Mexico (Pike, 1962). Satellite coverage of the onset of winter ice cover in the Bering Strait may help explain the environmental signals that initiate the southern migration. Other marine mammals that are important in the region, and that undergo long-distance movements, include: Northern fur seal, *Callorhinus ursinus*, migrating between summer breeding grounds on the Pribilof Islands in the eastern Bering Sea (and on other islands around the Northern Pacific rim) and wintering areas in the Gulf of Alaska and off the U.S. Pacific coast (Fiscus, 1978); humpback whale, *Megaptera novaeangliae*, an endangered species of which the eastern Pacific stock migrates between breeding and calving areas in the Hawaiian Islands and summer feeding grounds in the inland waters of southeastern Alaska (Wolman, 1978); and a number of species of dolphins and porpoise.

Allocation of Sampling Effort

Annual egg and larva surveys of northern anchovy are a regular activity of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each survey requires 4-5 weeks of ship time to make vertical net tows at 800-900 stations. The accuracy of the estimate of spawning biomass derived from each survey depends on complete coverage of the geographic range of the spawning stock. Without a priori knowledge of this distribution, many extra stations beyond the range limits must be sampled to ensure adequate coverage. We are now investigating the use of satellite imagery to plan egg surveys based on environmental limits characterizing the spawning habitat and detectable from satellites, as described above.

The 1983 survey plan was modified during the cruise using information from satellites. When the cruise began north of Point Conception in February, eggs were found much farther north and offshore than in recent years. Upon examination of AVHRR temperature imagery, we realize that this extension of the spawning range was due to the 1982-83 El Niño event. The cold-water boundary which normally limits

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R. Lynn. 1984. Southwest Fisheries Center, ational Marine Fisheries Service, NOAA, .O. Box 271, La Jolla, Ca 92038. Pers. commun.

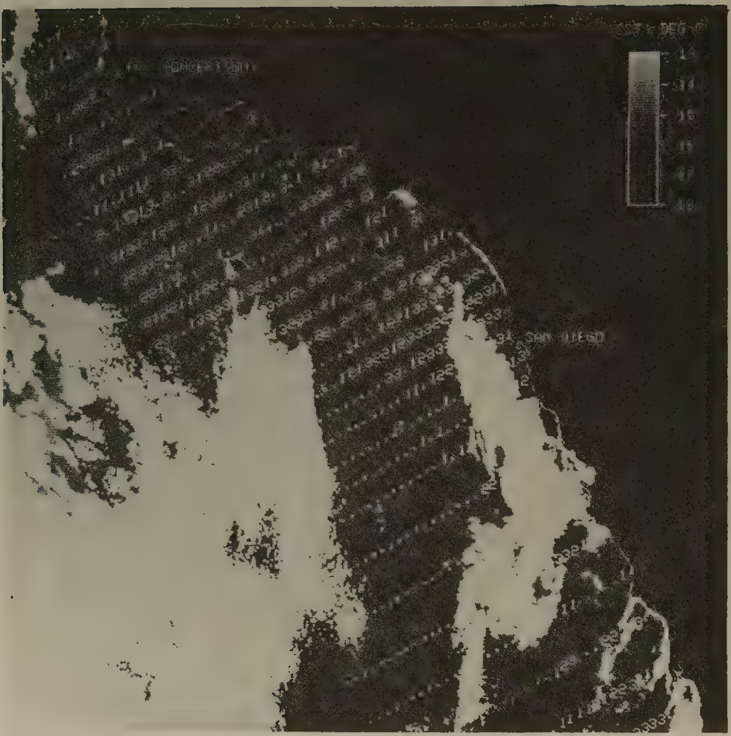

Figure 9.—Northern anchovy egg distribution, 9 February-29 March 1983: •=0, 1=1-3, 2=4-12, 3=13-229 eggs/0.05 m². Sea surface temperature (°C) from NOAA-7 AVHRR, 10 February 1983.

spawning to the southeast of Point Conception had shifted to the north and offshore (Fig. 9, compare with Fig. 3). As a result, the lines of sampling stations were extended farther offshore than originally planned, to ensure coverage of the entire spawning stock.

In another study conducted in June 1980 on the feeding biology of larval jack mackerel, satellite data were used to locate an intensive sampling grid on a temperature front. The front was observed southwest of San Diego in a NOAA-6 AVHRR image obtained over 1 week prior to the cruise, and it persisted during the sampling period (Fig. 10). The front was subsequently found to be related to an important gradient in food availability[4].

These two examples demonstrate how a single satellite image, from data received and processed in a matter of hours, can save days of ship time by locating significant environmental features and permitting efficient allocation of sampling effort. The potential cost savings are obvious, but the real-time use of satellite data requires facilities for direct reception and processing.

Fisheries Aid Charts

Operational applications of satellite data to commercial fishing activities

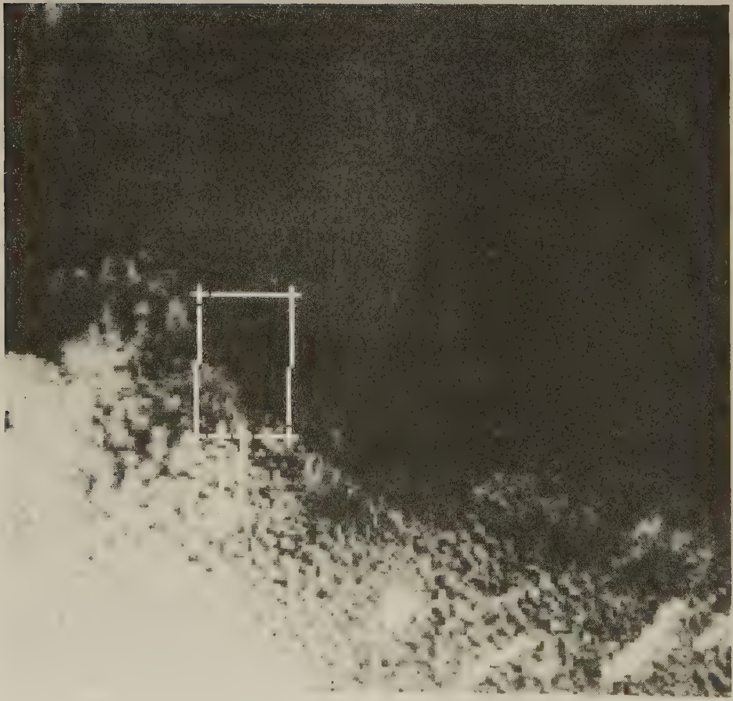

Figure 10.—Uncalibrated NOAA-6 AVHRR channel 4 image off southern California, 5 June 1980. Lighter shades represent cold sea surface temperatures, clouds appear white. Box encloses a 30 × 67 km grid of 41 stations centered at lat. 31° N, long. 120°30′ W.

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[4] R. Hewitt. 1983. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038. Pers. commun.

began along the Pacific coast in 1975 (Breaker, 1981) and have now been extended to Alaska. Charts showing sea surface temperature fronts and sea ice visible in satellite AVHRR images, and surface isotherms mapped from satellite and ship data, are produced routinely by NOAA (Fig. 11). The Northwest Ocean Services Center in Seattle produces a chart covering northern California, Oregon, Washington, and southern British Columbia, from lat. 40°N to lat. 52°N. The Satellite Field Services Station in Redwood City, Calif., produces a chart covering central and southern California and northern Baja California, from lat. 28°N to lat. 40°N. Coverage of both charts extends offshore to long. 135°W. They are produced once or twice weekly year-round and are distributed primarily by radio facsimile from the U.S. Coast Guard

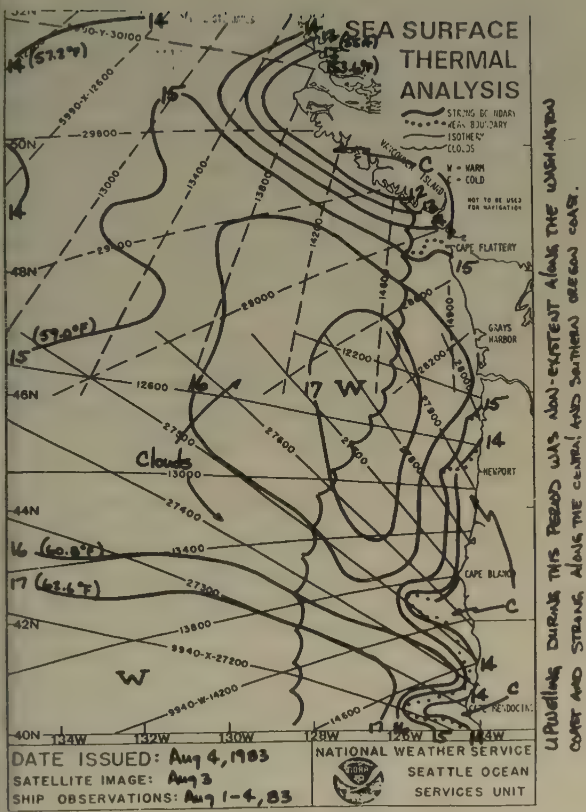
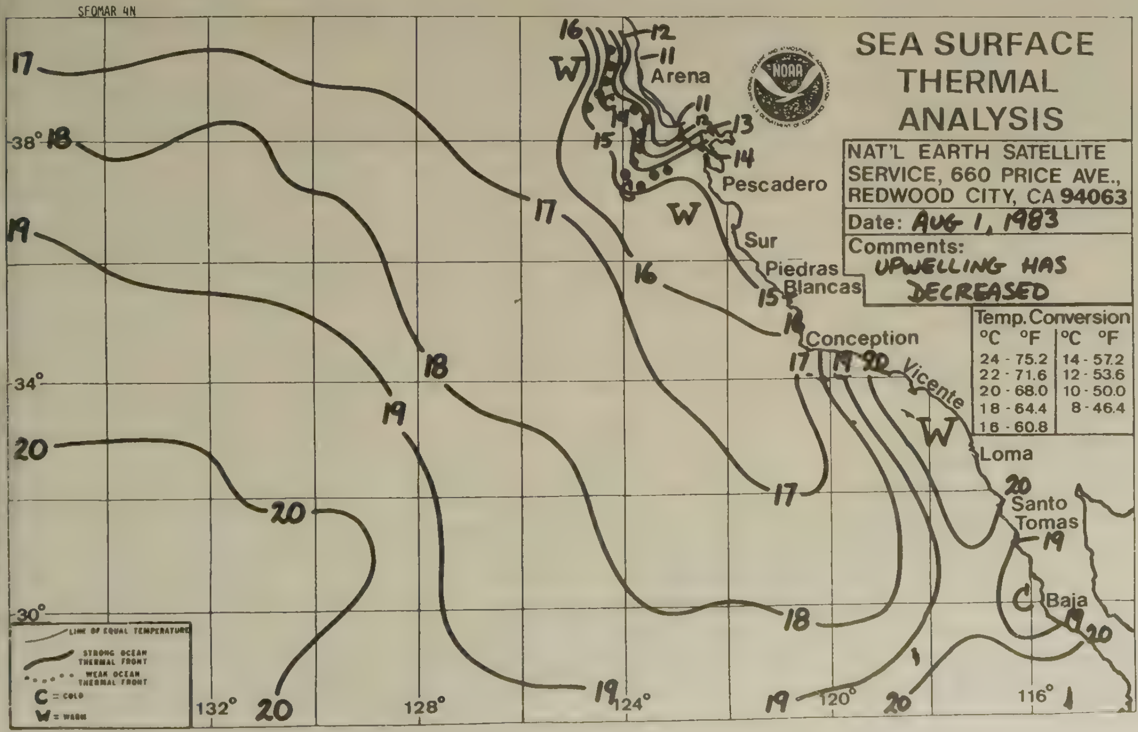

SEA SURFACE
THERMAL
ANALYSIS
STRONG BOUNDARY
WEAK BOUNDARY
ISOTHERM
CLOUDS
W = WARM
C = COLD
NOT TO BE USED FOR NAVIGATION
VANCOUVER ISLAND
CAPE FLATTERY
GRAYS HARBOR
NEWPORT
CAPE BLANCO
CAPE MENDOCINO
Clouds
(57.2°F)
(59.0°F)
16 (60.8°F)
17 (62.6°F)
50N
48N
46N
44N
42N
40N
134W
132W
130W
128W
126W
124W
DATE ISSUED: Aug 4, 1983
SATELLITE IMAGE: Aug 3
SHIP OBSERVATIONS: Aug 1-4, 83
NATIONAL WEATHER SERVICE
SEATTLE OCEAN SERVICES UNIT
UPWELLING DURING THIS PERIOD WAS NON-EXISTENT ALONG THE WASHINGTON COAST AND STRONG ALONG THE CENTRAL AND SOUTHERN OREGON COAST.

Figure 11.—Sea surface temperature charts produced by the National Weather Service.


SFOMAR 4N
SEA SURFACE
THERMAL
ANALYSIS
NAT'L EARTH SATELLITE
SERVICE, 660 PRICE AVE.,
REDWOOD CITY, CA 94063
Date: AUG 1, 1983
Comments:
UPWELLING HAS DECREASED
Temp. Conversion
°C °F
24 - 75.2
22 - 71.6
20 - 68.0
18 - 64.4
16 - 60.8
14 - 57.2
12 - 53.6
10 - 50.0
8 - 46.4
Arena
Pescadero
Sur
Piedras Blancas
Conception
Vicente
Loma
Santo Tomas
Baja
38°
34°
30°
132°
128°
124°
120°
116°
LINE OF EQUAL TEMPERATURE
STRONG OCEAN THERMAL FRONT
WEAK OCEAN THERMAL FRONT
C = COLD
W = WARM

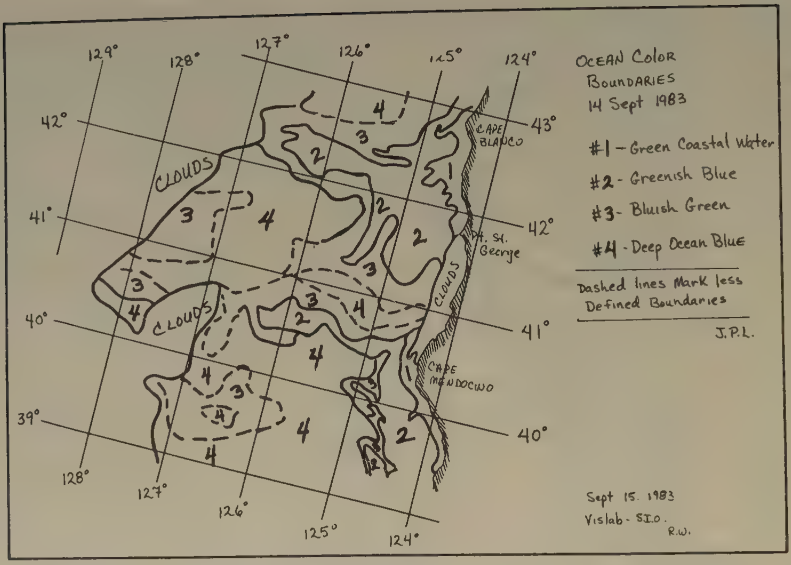


Figure 12.—Ocean color boundary chart off northern California and Oregon (R. Wittenberg, Scripps Visibility Laboratory).

radio station at Point Reyes, Calif. Fishermen use these charts to save time in searching for productive fishing areas associated with frontal features.

The Alaska Ocean Services Unit, located in Anchorage, produces charts covering British Columbia, the Gulf of Alaska, Aleutian Islands, eastern Bering Sea, Chukchi Sea, and Beaufort Sea, from lat. 48°N to lat. 75°N. Charts showing sea surface temperature and sea ice are distributed three times a week; these are intended to aid the safety and efficiency of fishing. Other charts showing 3-and 5-day sea ice forecasts are also distributed daily in winter. Both types of charts are issued by radio facsimile from the U.S. Coast Guard Station at Kodiak, Alaska.

Ocean color boundary charts have been produced experimentally from CZCS data since 1981 in a NASA/Jet Propulsion Laboratory program (Montgomery, 1981). The charts delineate strong gradients in the blue/green color ratio (channel 1/channel 3 radiance). In 1983, charts were produced at almost weekly intervals from May to October (18 charts total), covering coastal areas up to 700,000 km² between Vancouver Island, B.C., and Guadalupe Island, Mex. (Fig. 12). A chart was produced only when a large, cloud-free area was located in a Nimbus-7 pass. The chart was then broadcast on the same or following day to fishing boats by radio facsimile from Point Reyes and La Jolla, Calif. Color photographs of the satellite images were distributed by express mail to various fishing ports and to Sea Grant marine advisors in daily contact with fishermen. The color boundary charts and photographs are used by albacore and salmon fishermen. These fish are sometimes found aggregated along color fronts which do not correspond to temperature fronts.

Conclusions

Satellites have altered our perceptions of the ocean environment through the extensive spatial coverage, temporal continuity, and high resolution of the data they provide. Limited, but useful, applications to several types of problems in fisheries research and operations have been demonstrated. Continued development of these and other applications will depend on inexpensive and convenient access to data and data-processing facilities. Recent trends in the federal budget have not been encouraging. For instance, there are no current prospects for a new ocean color scanner to replace the aging CZCS on Nimbus-7. The commercial utility of satellite data depends largely on near real-time availability to fishermen and other maritime users. In the future, this demand may be met by processed satellite data products tailored more to particular user needs.

Acknowledgments

This work was supported jointly by the Southwest Fisheries Center, La Jolla, Calif., and the Northwest and Alaska Fisheries Center, Seattle, Wash., as a cooperative research project. We thank the many persons who contributed information and ideas for various applications, as well as those who provided technical support at the Scripps Satellite Oceanography Facility and the Scripps Visibility Laboratory. Processing of CZCS data was supported by NASA order W15,334.

Literature Cited

Anonymous. 1984. 1983 in review. Pac. Fish. 1984 Yearb.

Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake, *Merluccius productus*. Mar. Ecol. Prog. Ser. 6:1-9.

Bakkala, R., W. Hirschberger, and K. King. 1979. The groundfish resources of the eastern Bering Sea and Aleutian Island regions. Mar. Fish. Rev. 41(11):1-24.

Bakun, A., and R. H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep. 23:99-112.

Bernstein, R. L. 1982. Sea surface temperature estimation using the NOAA-6 satellite Advanced Very High Resolution Radiometer. J. Geophys. Res. 87:9455-9465.

________, L. Breaker, and R. Whritner. 1977. California Current eddy formation: Ship, air, and satellite results. Science 195:353-359.

Borstad, G. A., R. M. Brown, D. Truax, T. R. Mulligan, and J. F. R. Gower. 1982. Remote sensing techniques for fisheries oceanography: Examples from British Columbia. NAFO Sci. Counc. Studies 4:69-76.

Braham, H. W., M. A. Fraker, and B. D. Krogman. 1980. Spring migration of the western Arctic population of bowhead whales. Mar. Fish. Rev. 42(9-10):36-46.

Breaker, L.C. 1981. The application of satellite remote sensing to west coast fisheries. J. Mar. Tech. Soc. 15:32-40.

Burns, J. J., L. H. Shapiro, and F. H. Fay. 1981. Ice as marine mammal habitat in the Bering Sea, p. 781-797. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: Oceanography and resources, Vol. 2. Univ. Wash. Press, Seattle.

Fay, F. H. 1974. The role of ice in the ecology of marine mammals of the Bering Sea, p. 383-399. *In* D. W. Hood and E. J. Kelly (editors), Oceanography of the Bering Sea with emphasis on renewable resources, Univ. Alaska, Fairbanks, Inst. Mar. Sci. Occas. Publ. 2.

Fiedler, P. C. 1983. Satellite remote sensing of the habitat of spawning anchovy in the Southern California Bight. (CalCOFI Rep. 24:202-209.

________. 1984. Satellite observations of the 1982-83 El Niño along the U.S. Pacific coast. Science 224:1251-1254.

Fiscus, C. H. 1978. Northern fur seal, p. 153-159. *In* D. Haley (editor), Marine mammals of eastern North Pacific and Arctic waters. Pac. Search Press, Seattle.

Gordon, H. R., D. K. Clark, J. W. Brown, O. B. Brown, R. H. Evans, and W. W. Broenkow. 1983. Phytoplankton pigment concentrations in the Middle Atlantic Bight: Comparison of ship determinations and CZCS estimates. Appl. Opt. 22:20-36.

Gower, J. F. R. 1982. General overview of the nature and use of satellite remote sensing data for fisheries application. Northwest Atl. Fish. Organ., Sci. Counc. Studies 4:7-19.

Hartt, A. C. 1980. Juvenile salmonids in the oceanic ecosystem—the critical first summer, p. 25-57. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific. Oreg. State Univ. Press, Corvallis.

Hayman, R. A., and A. V. Tyler. 1980. Environment and cohort strength of Dover sole and English sole. Trans. Am. Fish. Soc. 109:54-70.

Husby, D. M., and C. S. Nelson. 1982. Turbulence and vertical stability in the California Current. CalCOFI Rep. 23:113-129.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: Contrasting years, 1975-1978. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178: 375-388.

________, J. Peláez, and R. M. Laurs. 1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (*Engraulis mordax*). Remote Sensing Environ. 11:439-453.

Laurs, R. M., and R. J. Lynn. 1977. Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: Distribution, relative abundance, and association with Transition Zone waters. Fish. Bull., U.S. 75:795-822.

________, and J. T. Brucks. In Press. Living marine resources applications of satellite imagery. *In* B. Saltzman (editor), Satellite Remote Sensing in Oceanography. Advances in Geophysics, Acad. Press, N.Y.

________, P. C. Fiedler, and D. R. Montgomery. In Press. Albacore tuna catch distributions relative to environmental features observed from satellites. Deep-Sea Res.

McClain, E. P., W. G. Pichel, C. C. Walton, Z. Ahmad, and J. Sutton. 1983. Multichannel improvements to satellite-derived global sea surface temperatures. Adv. Space Res. 2:43-47.

McNutt, S. L. 1981. Remote sensing analysis of ice growth and distribution in the eastern Bering Sea, p. 141-165. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: Oceanography and resources, Vol. 1. U.S. Gov. Print. Off., Wash., D.C.

Mathews, S. B. 1980. Trends in Puget Sound and Columbia River salmon, p. 133-145. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, Oreg. State Univ. Press, Corvallis.

Miller, D. R., J. G. Williams, and C. W. Sims. 1983. Distribution, abundance and growth of juvenile salmonids off the coast of Oregon and Washington, summer 1980. Fish. Res. 2:1-17.

Montgomery, D. R. 1981. Commercial applications of satellite oceanography. Oceanus 24(3):56-65.

NASA Satellite Wind Stress Working Group. 1982. Scientific opportunities using satellite wind stress measurements over the ocean. Nova Univ./N.Y.I.T. Press, Fort Lauderdale, Fla., 153 p.

Nelson, C. S., and D. M. Husby. 1983. Climatology of surface heat fluxes over the California Current region. NOAA Tech. Rep. NMFS SSRF-763, 155 p.

Otto, R. S. 1981. Eastern Bering Sea crab fisheries, p. 1037-1066. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: Oceanography and resources, Vol. 2. Univ. Wash. Press, Seattle.

Pike, G. C. 1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). J. Fish. Res. Board Can. 19:815-838.

Poole, F. W., and G. L. Hufford. 1982. Meteorological and oceanographic factors affecting sea ice in Cook Inlet. J. Geophys. Res. 87(C3):2061-2070.

Sadler, J. C., L. Oda, and B. J. Kilonsky. 1976. Pacific Ocean cloudiness from satellite observations. Univ. Hawaii, Honolulu, 137 p.

Smith, R. C. 1981. Remote sensing and depth distribution of ocean chlorophyll. Mar. Ecol. Prog. Ser. 5:359-361.

________, and K. S. Baker. 1982. Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 Coastal Zone Color Scanner). Mar. Biol. 66:269-279.

Van Woert, M. 1982. The subtropical front: Satellite observations during FRONTS 80. J. Geophys. Res. 87:9523-9536.

Wahle, R. J., and W. S. Zaugg. 1982. Adult coho salmon recoveries and their Na^+-K^+ ATPase activity at release. Mar. Fish. Rev. 44(11):11-13.

Weeks, W. F. 1981. Sea ice: the potential of remote sensing. Oceanus 24(3):39-48.

Wolman, A. A. 1978. Humpback whale, p. 47-53. *In* D. Haley (editor), Marine mammals of eastern North Pacific and Arctic waters. Pac. Search Press, Seattle.

Yamanaka, I. 1982. Application of satellite remote sensing to fishery studies in Japan. NAFO Sci. Counc. Studies 4:41-50.

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Journal of Marine Research, 43, 907–924, 1985

Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment

by Amatzia Genin[1] and George W. Boehlert[2]

ABSTRACT

Three hydrographic surveys comprised of densely spaced XBT and CTD stations were conducted over Minami-kasuga Seamount, in the northwest Pacific (21°36′N, 143°38′E). A cold dome, similar to a Taylor column, was observed above the seamount top during the first survey. Uplifted isotherms penetrated to the lower euphotic zone and were associated with higher chlorophyll concentrations. Vertical displacement of uplifted isotherms decayed with elevation above the seamount, so that both temperature and chlorophyll anomalies were undetectable at depths less than 80 m. Relatively high chlorophyll concentrations in a layer from 80 m to 100 m depth formed a distinctive deep chlorophyll maximum (DCM) which was less well defined away from the seamount. Calculations based on the observed chlorophyll increase and on estimated phytoplankton growth rate suggested a minimal residence time of the cold dome on the order of several days. Zooplankton densities were also higher over the seamount top, both within and above the cold dome. No cold dome, chlorophyll increase, or high zooplankton biomass were detected above the seamount on the second and third surveys, carried out 2 and 17 days later, respectively. Mixing and deflections of isotherms occurred within a "boundary zone" around the seamount slope during the first and third surveys.

Our observations suggest that seamounts are a source of both biological and physical patchiness in the surrounding ocean as features developed above them are swept away. The importance of the seamount-generated "experiment" is discussed in relation to field studies of the DCM. Specifically, our observations suggest that a sharp chlorophyll maximum can be formed by enhanced *in situ* growth following a sub-surface upwelling event.

1. Introduction

Recent studies of the interactions between seamounts and ocean currents have provided considerable evidence for the occurrence of unique physical phenomena at these habitats. Local deflections of isotherms, usually in the form of uplifting, have been observed above several seamounts at different locations and depths (Meincke, 1971; Vastano and Warren, 1976; Fukasawa and Nagata, 1978; Owens and Hogg, 1980; Gould *et al.,* 1981; Roden and Taft, 1985). The Taylor column theory (Taylor,

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1923; Hogg, 1973; Huppert, 1975; Huppert and Bryan, 1976) predicts the occurrence of such deflections as a result of the encounter between a current and a seamount in which water from below the summit depth flows above the topographic obstacle. Vortex lines above the seamount are compressed, and due to conservation of potential vorticity anticyclonic vorticity is induced. The resulting flow-field is a combination of the velocity induced by the anticyclonic vorticity and the free-stream velocity. Under certain conditions of current, stratification, and topography, a closed-streamlined anticyclonic vortex, or a Taylor column, comprised of relatively deep upwelled water, is expected to remain trapped above the seamount (Hogg, 1973; Huppert, 1975). A few field observations of Taylor columns have been reported (Owens and Hogg, 1980; Gould *et al.,* 1981; Eide, 1979), but no work so far has examined the biological consequences of this phenomenon.

Seamount-induced upwelling may affect local biological processes in the overlying waters, depending upon its vertical extent above the topography and the residence time of the upwelled waters within the trapped vortex. In oligotrophic oceans, phytoplankton production would increase if the uplifted isotherms penetrated into the euphotic zone, replenishing its depleted water with nutrients. Such local enrichment can proceed along the trophic chain as a function of the residence time of the upwelled water above the seamount. Entrapment on the order of a day(s) (i.e., comparable to a typical generation time of phytoplankton) would probably affect only the primary producers, and hence, a patch of relatively high chlorophyll concentrations would be associated with the physical structure. A longer residence time, on the order of several weeks, may locally affect the growth and abundance of zooplankton species. Lagrangian current observations made above the Emperor Seamounts (Cheney *et al.,* 1980) and the Corner Rise Seamounts (Richardson, 1980) suggested entrapment periods up to several weeks within seamount-generated anticyclonic eddies. Much longer periods (on the order of several months) were inferred from hydrographic and Eulerian current measurements above a deep seamount in the North Atlantic (Owens and Hogg, 1980). If local enrichment persists for long periods, and if it is a recurrent phenomenon, nektonic organisms may be attracted to or aggregated in these habitats, and demersal predatory species may proliferate there (Boehlert and Seki, 1984). It is well known that many seamounts are excellent fishing sites for both pelagic nekton, such as tuna, and several epibenthic species (Uda and Ishino, 1958; Hubbs, 1959; Herlinveaux, 1971; Hughes, 1981; Uchida and Tagami, 1984; Boehlert, in review).

The local modification of physical and biological conditions by a mid-oceanic seamount has a unique methodological importance. Experimental manipulations commonly performed in marine intertidal and subtidal research (see reviews by Connell, 1974; Dayton and Oliver, 1980) have significantly contributed to the understanding of key ecological processes. Unfortunately, such manipulations cannot be reasonably performed on scales large enough to be applicable to the open ocean. Warm- and cold-core rings have provided natural experiments in which isolated

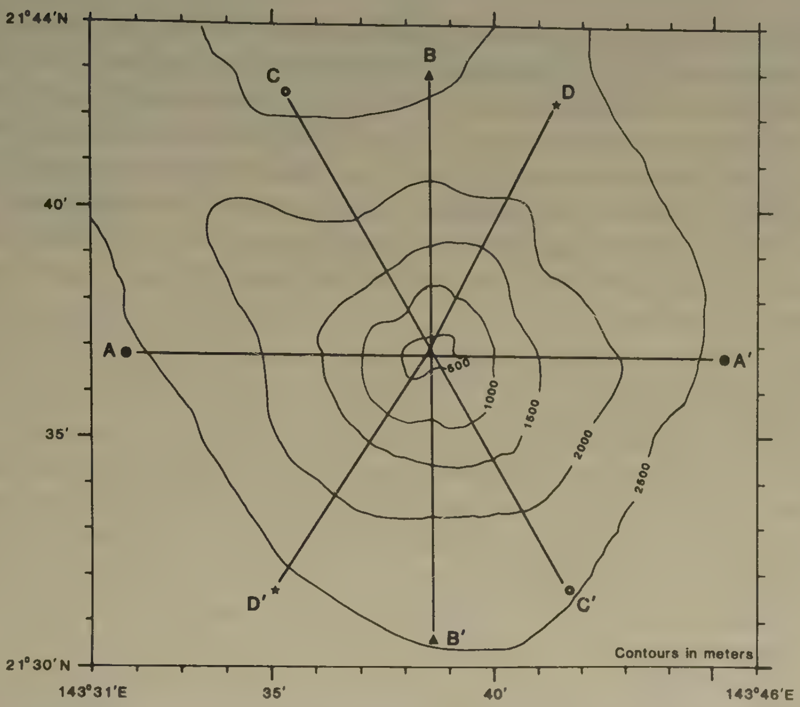

Figure 1. Bathymetry of Minami-kasuga Seamount and survey transect lines. The first two surveys were comprised of transect lines AA′ and BB′; the third survey was comprised of lines AA′, CC′, and DD′. A detailed bathymetric chart of the seamount has been published by Hussong and Fryer (1983).

pelagic populations have been studied (Backus *et al.,* 1981; Olson and Backus, 1985). Seamount-induced upwelling may provide similar "manipulations"; for example, changes of chlorophyll profiles induced by seamount-generated upwelling may help us understand processes related to the formation and maintenance of the deep chlorophyll maximum (DCM). In addition, relationships between different time scales and the trophic level of the associated biological response make the biological investigation useful for understanding temporal characteristics of the relevant physical processes. In this paper we describe the physical and biological dynamics in the waters overlying a seamount in the northwest Pacific, compare the observed features to criteria of the Taylor column theory, and discuss the implications of the results to several problems in biological oceanography.

2. Study site

Minami-kasuga Seamount (21°36′N, 143°38′E, 260 m minimum depth; Fig. 1), is located in the Mariana Ridge about 180 km north-west of Farallon de Pajaros, the northernmost island on the ridge. Surveys carried out by Japanese vessels (Hokkaido

University, 1967, 1968, 1969—about 200 km east of the seamount; Japan Oceanographic Data Center 1977–1979,—about 550 km east of the seamount) exhibit warm and oligotrophic conditions; sea-surface temperatures are between 24° to 25°C, surface chlorophyll concentrations of about 0.1 mg m^{-3}, and integrated primary production values (^{14}C uptake) range from 0.1 to 0.5 gC m^{-2} day^{-1}. An euphotic zone of about 100 m to 130 m deep is characterized by nitrate and phosphate concentrations typically lower than 0.1 μg/1. The nutricline is usually deeper than 100 m. Additional characteristics of Minami-kasuga Seamount region, relevant to Taylor column theory, are described in Section 4.

3. Materials and methods

Three XBT/CTD surveys across the seamount were performed on 13, 15, and 30 March 1984. Each survey consisted of 2 (during the first two surveys) or 3 (during the third survey) 22 km-long transects, centered above the seamount top (Fig. 1). Each transect along line AA′ (Fig. 1) included a CTD station at each end, one to three CTD stations above the top, and XBT stations in between, so that the distance between adjacent temperature profiles was 2.5 km or less. All other transects were comprised of XBT stations, except line BB′ of the first survey, which included CTD's at its ends, and line CC′ of the third survey, which included CTD's at both its center and end stations. CTD Model 9041 (Plessey Environmental Systems, California) and XBT's Model T-4 (Sippican Corp., Massachusetts) were used throughout the cruise. Water samples were collected at all CTD stations with twelve 1.7 1 Niskin bottles mounted on the CTD rosette. Chlorophyll *a* concentrations, retained on GF/C filters, were determined fluorometrically (Yentsch and Menzel, 1963; Holm-Hansen *et al.*, 1965), using a Turner model 111 fluorometer.

The depth channel of the CTD magnetic tape recorder malfunctioned during the first two surveys, and the analog chart records were therefore used to analyze the temperature profiles. The error of this procedure was estimated from data of the third survey, when the depth channel did function. Comparison of analog- to digital-recorded depths showed that the former values were greater by a mean (±SD) of 3.1 ± 3.3 m than the latter values. Chart-inferred depths of the first and second survey were corrected accordingly. Density during these surveys was calculated by matching tape-recorded salinity and temperature values with chart-recorded depths which corresponded to the same temperature values. Time series of temperature–salinity data taken at two stations in the region (21N, 137E; and 22N, 137E) from 1974 to 1977 (Japan Oceanographic Data Center, 1977–1979) demonstrated that temperatures between 10°C – 22°C are good indicators of salinity. Similar T-S relationships have also been reported for the general region (Fig. 8 in Emery and Dewar, 1982). Temperatures were therefore used throughout this work as the principal physical parameter, representing water density.

Zooplankton tows above the seamount and in the deep ("control") areas were made with an opening-closing 1 m^2 Tucker trawl with 0.333 mm mesh deployed as described by Boehlert *et al.* (1985). Five tows were carried out during the first survey, and three tows during the third survey. Samples were taken in two depth ranges, from 150 m to the bottom of the mixed layer and from there to the surface. If the bottom of the mixed layer was indistinct, tows were divided at 80 m; all division points were thereby in the depth range of 60 m to 85 m. All tows were performed at night in order to minimize the effects of avoidance and diurnal migration on our estimates of zooplankton biomass.

4. Results and discussion

a. First survey (March 13, 1984). Uplifted isotherms formed a sub-surface cold dome above the seamount top (Fig. 2a). The vertical displacement of the uplifted isotherms gradually decreased with elevation above the seamount, from a 50 m uplift of the 17°C isotherm close to the substratum, to a decay of the cold anomaly at a level of about 80 m depth (180 m above the seamount top). Different deflection trends of isotherms in the vicinity of the substratum around the seamount slope formed a "boundary zone" comprised of three distinctive layers: a layer of downward deflected isotherms from approximately 500 m to about 420 m deep; a relatively well-mixed "transition zone" (Fig. 2b) between the 14.5°C and 15°C isotherms, approximately 50 m above the previous layer; and an upwelling layer shallower than 340 m depth.

Several parameters of the physical structure can be used to compare our observations with theoretical criteria for the existence of a closed-streamline Taylor column. The model (Hogg, 1973; Huppert, 1975; Huppert and Bryan, 1976) considers a water column, of total depth H, in which bottom water (i.e., from depth H) is flowing over a seamount of height h. In our case, H would thereby be the depth of the base of the upwelling (340 m), and the relevant seamount height, h, would be the altitude of the seamount top above this base (80 m). The width of the observed cold dome at the depth of the seamount (approximately 5.5 km) was thereby considered as the typical horizontal scale (L). Vertical variation of stratification strength caused a gradual decrease of the buoyancy frequency, N, from $1.79 \times 10^{-3}\ s^{-1}$ in the upper thermocline to $1.13 \times 10^{-3}\ s^{-1}$ at the depth of the seamount top, with a mean of $1.35 \times 10^{-3}\ s^{-1}$ for the entire depth range of the cold dome (N values were calculated at the control station C5). Coriolis parameter at the seamount latitude is $5.34 \times 10^{-5}\ s^{-1}$, and the relevant Rossby number, R, was $U/29.4$ (where U is the upstream velocity in cm s^{-1}). A critical criterion for the existence of a closed-streamline Taylor column (Huppert, 1975; Owens and Hogg, 1980) is the value of the non-dimensional height h_o/R (where h_o is the scaled seamount height h/H). No closed-streamline occurs when the seamount height is too low (lower h_o) or the oncoming flow is too strong (higher R). The critical h_o/R value for Minami-kasuga Seamount is 1.4 (Fig. 3 of Huppert [1975], using the mean value of N). Hence, a Taylor column, similar to the observed cold dome would occur when R is smaller than 0.16, or when the upstream velocity is about 5 cm s^{-1} or less. Much lower velocities, however, would not have sufficient energy to lift the water

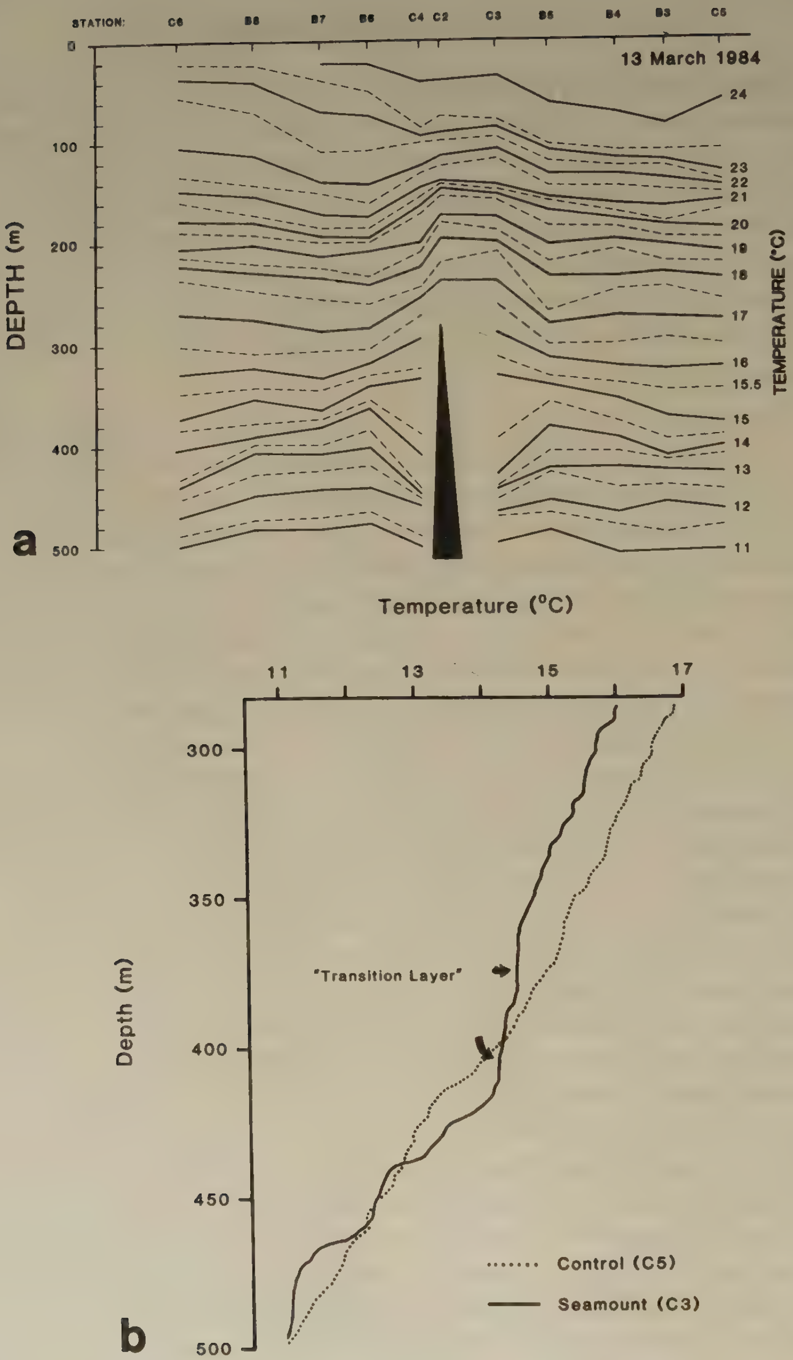

Figure 2. The first survey. (a) temperature structure along transect line AA′. Similar temperature structure at the deep area was observed along transect line BB′, which did not include CTD stations above the seamount top. Note that the vertical scale is 50 times greater than the horizontal scale. (b) expanded temperature profiles in the boundary zone close to the seamount (station C3) and at a station about 11 km to the east of the seamount (C5). The "transition" layer at C3 is comprised of two steplike structures, of which the upper one is isothermal and the lower one is characterized by a very gradual gradient. (c) chlorophyll *a* profiles above the seamount top (right) and in the control stations (left).

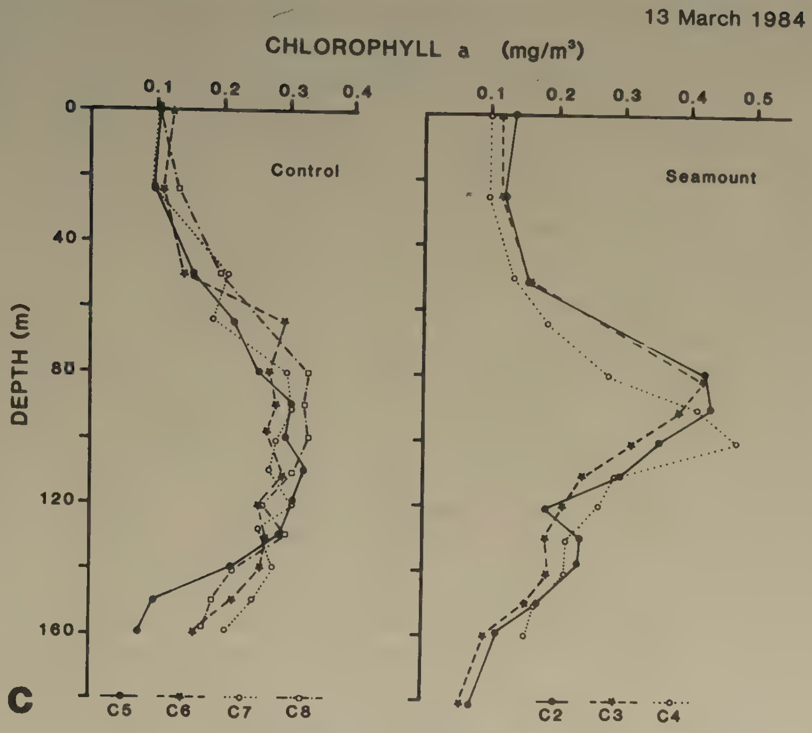

Figure 2. (Continued)

through a vertical displacement comparable to the height, *h*, of the seamount; Huppert and Bryan (1976) have found that in the case of strong stratification the amplitude of the disturbance in the vicinity of the topographic feature is dependent on the parameter Nh/U. Stronger stratification (higher N) would require higher upstream velocity to upwell water above a seamount top. For the stratification strength found at the depth of Minami-kasuga Seamount top and for the previously calculated critical velocity of 5 cm s^{-1}, the value of Nh/U is about 1.8, which is on the order of the critical value (Huppert and Bryan, 1976) required for water from 340 m to flow above the seamount top. An additional effect of stratification is to confine the vertical extent of the cold anomaly near the bottom. A decay of the seamount-induced deflections is expected at a height fL/N above the top (Huppert, 1975; Owens and Hogg, 1980); that is, for stronger stratification (greater N) the cold anomaly would decay closer to the bottom. The observed height of the cold dome above the seamount (approx. 180 m) is in good agreement with the theoretically-predicted range of 164 m (using N value of the upper thermocline) to 260 m (using N value at the level of the seamount top).

Three chlorophyll profiles, taken within the cold dome, showed a distinctive maximum between 80 and 100 m depth; the chlorophyll maximum layer at the four control stations was comparatively diffuse (Fig. 2c). The causal relationships between

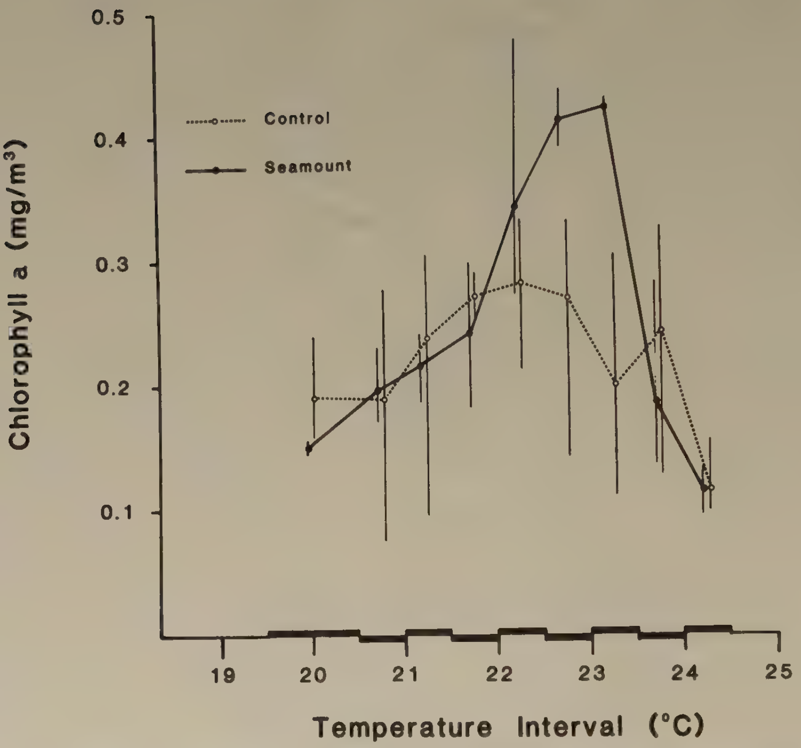

Figure 3. Chlorophyll—temperature diagram of the first survey. The mean (circle) and range (vertical bar) of the chlorophyll concentrations in each temperature interval (horizontal bar on the abscissa) are plotted for the seamount stations (solid line) and control stations (dashed line).

the localized upwelling and the biological response are corroborated by the confinement of the chlorophyll increase to depths below 80 m, the uppermost edge of the cold dome. The chlorophyll concentrations at shallower depths varied little throughout the area, both above the seamount and at the control stations. "Hardness" values (maximum chlorophyll concentration divided by the mean, Dandonneau, [1979]), which reflect the sharpness of chlorophyll profiles, were significantly higher ($p < 0.05$, Mann-Whitney *U*-test) in the seamount stations (mean [±SD] = 2.08 ± 0.16) than in the control stations (1.49 ± 0.13). This reflected a mean increase of 50% in chlorophyll concentrations in the 80 to 100 m depth interval.

Temperature versus chlorophyll diagrams (Fig. 3) revealed that the chlorophyll increase was confined to waters between 22°C to 23.5°C, where concentration increases for a given water temperature ranged from 21% to 112% with a mean of 62%. The chlorophyll increase, however, did not significantly affect the integrated chlorophyll values in the upper 160 m (the means [±SD] for the control and seamount stations were 35.88 ± 2.4 and 36.45 ± 1.5 mg Chl *a* m^{-2}, respectively; $p > 0.1$, *t*-test).

This similarity in the integrated values was apparently due to high variability of the concentrations at depths below the DCM and to the confinement of the chlorophyll increase to a rather narrow layer.

Estimates of the time necessary for the formation of the observed chlorophyll maximum at the seamount stations can be used to calculate a minimum residence time of the hypothesized Taylor column. Although the chlorophyll:biomass ratio in phytoplankton is by no means constant (see review by Cullen, 1982), several studies have shown that the increase of chlorophyll in grazer-free incubation experiments is an adequate variable for estimating phytoplankton growth, giving similar values to those obtained by other techniques (Thomas, 1970; Redalje and Laws, 1981; Furnas, 1982; Bienfang and Takahashi, 1983; Laws *et al.,* 1984). Estimates of phytoplankton growth rates in oligotrophic waters, however, vary considerably among different investigators and techniques (see reviews by Goldman *et al.,* 1979; Eppley, 1981), and efforts have recently been made to resolve this important controversy (Eppley, 1982). Growth rates found in two related multi-method experiments, carried out in the oligotrophic Hawaiian coastal waters were 0.29 doubling per day (station TT-157 of Welschmeyer and Lorenzen, 1985) and in the range of 0.95 to 2.88 doubling per day (Laws *et al.,* 1984). The latitude, hydrographic conditions, integrated primary production, and nutrient and chlorophyll profiles in those waters (Bienfang and Szyper, 1981) are similar to these found in the vicinity of Minami-kasuga Seamount. Applying these estimates of growth rate to the observed 50% to 60% increase of chlorophyll gives values of about 2.25 days (using the estimate of Welschmeyer and Lorenzen) or a range of 0.25 to 0.75 days (using the estimates of Laws *et al.*). These are most likely underestimated values since the unknown mortality rate due to zooplankton grazing (Jackson, 1980; Welschmeyer and Lorenzen, 1985) has not been included in our calculations. A lack of chlorophyll increase during the period between the occupation of the three seamount stations (C2 at 12:30, C3 at 14:15, and C4 at 17:30, Fig. 2c) further supports the assumption that the net growth rate within the cold dome was slower than those estimated by Laws *et al.* (1984). A crude estimate of the minimal time which had passed between the onset of upwelling above the seamount and our survey would therefore be on the order of days.

Zooplankton samples in this survey, although not duplicated, suggest a larger biomass over the seamount than at the control stations (Table 1). This observation is inconsistent with the possibility that the observed chlorophyll increase above the seamount was the result of reduced zooplankton grazing there. In contrast to the chlorophyll signal, zooplankton volumes were higher both within the cold dome and above it, and therefore might have been unrelated to the physical structure found above the top. Over Hancock Seamount (29°48′N, 179°04′E) where the summit depth is also 260 m, consistent decreases in larval fish densities were observed compared to a control station, even in 0–25 m tows (Boehlert, unpublished data).

An alternative explanation of our observations which cannot be refuted by the

Table 1. Zooplankton displacement volume (ml/1000 m^3) in the upper 150 m above the seamount top and in the control stations, during the first and third surveys. Approximate depth intervals of the strata are 150–80 m, and 80–0 m, for the deep and the shallow strata, respectively.

		Station				
	Stratum	Top	East	West	South	North
First Survey	Deep	73.8	40.0	49.3	43.6	42.2
	Shallow	88.5	56.2	61.9	48.9	59.2
Third Survey	Deep	29.8	43.0	33.9		
	Shallow	48.6	110.6	50.7		

present data is that the observed cold dome and the associated chlorophyll enrichment may simply be an oceanic "patch" which by chance was located above the seamount during our survey. Patchiness of different spatial scales in the ocean is a well documented phenomenon (e.g. Steele, 1977, and references therein), though its intensity in the oligotrophic central North Pacific is relatively low (McGowan and Walker, 1979). An adequate test of this alternative explanation against the Taylor column hypothesis would require deployment of an extensive array of current/temperature/fluorescence meters above and around the seamount. On the other hand, the location of the dome just above the seamount is consistent with other observations where seamount-generated upwelling was observed (Meincke, 1971; Vastano and Warren, 1976; Fukasawa and Nagata, 1978; Owens and Hogg, 1980; Gould *et al.*, 1981; Roden and Taft, 1985). Furthermore, the alternative explanation is weakened by the fact that no "patch" of a comparable spatial scale (several km) was found in any of the deep-water portions of the transects performed during our three surveys. These portions, nearly 100 km in total length, can be considered as a sample of the background patchiness. The ambient fluctuations of the 17°C to 20°C isotherms, for example, were almost an order of magnitude lower than their vertical displacement over the seamount (see below). The most important support, however, for explaining our observations in terms of the Taylor column theory is the agreement between the observed characteristics of the cold dome and the predictions and criteria of the theory, particularly its vertical decay and extent above the top.

b. Second survey (March 15, 1984). Neither cold dome nor chlorophyll increases were detectable along the transects of this survey (Fig. 4). The depths of the 17°C to 23°C isotherms and the chlorophyll profiles (mean [±SD] "Hardness" = 1.71 ± 0.36) were similar to those at the control stations of the first survey ($p > 0.1$ Mann-Whitney *U*-test, for the "Hardness" values). Quasihorizontal isotherms also characterized the benthic boundary zone around the seamount slope. A possible cause for this remark-

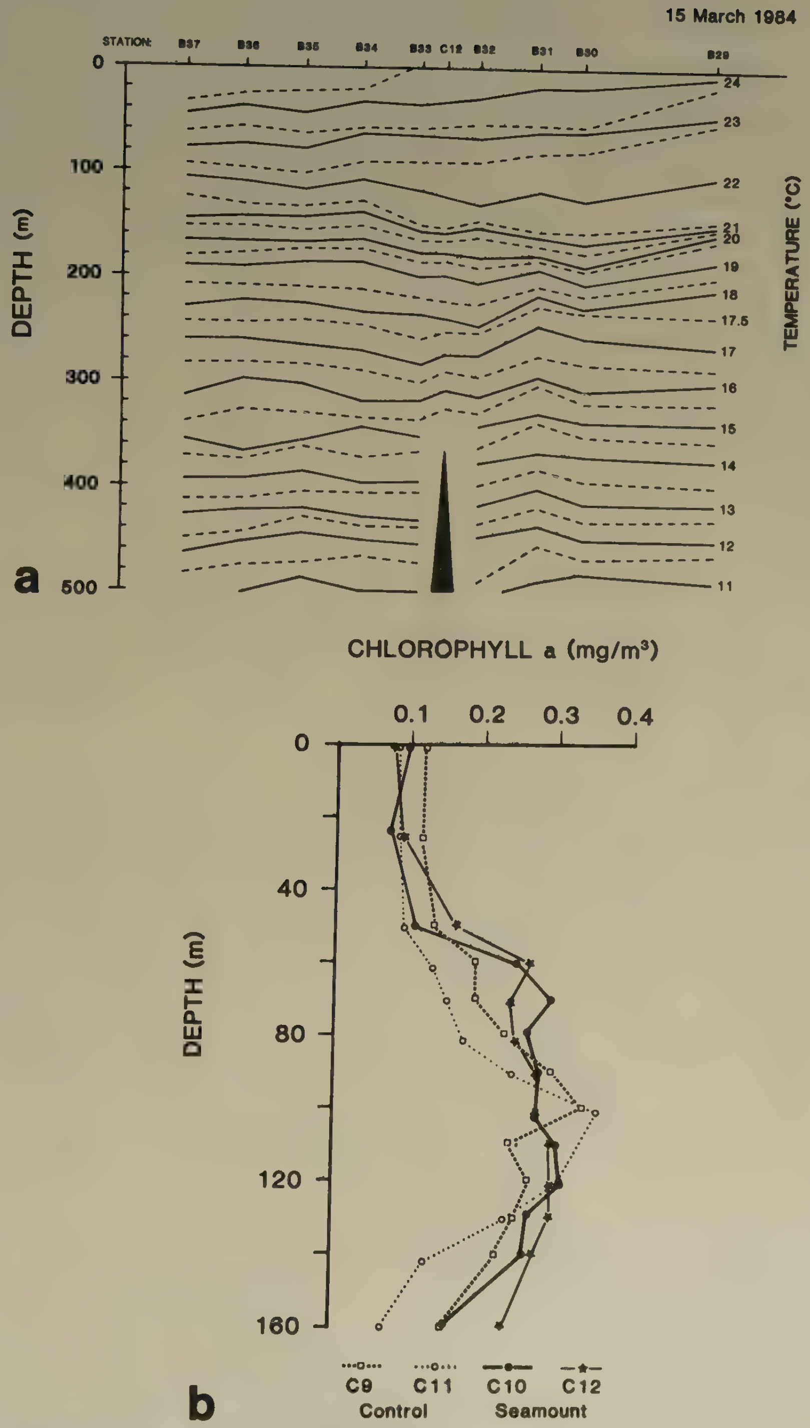

Figure 4. The second survey. (a) temperature structure along transect line BB′. A similar pattern was found along line AA′. (b) chlorophyll *a* profiles above the seamount top (solid lines) and in the control stations (dashed lines).

able difference between the two surveys is a change in the on-coming current velocity. An increase of the upstream velocity to about 20 cm s^{-1}, for example, which is a speed well within the range found at mid-ocean measurements at similar depths (e.g., record #7041 of Schmitz *et al.*, 1982—in the western North Pacific south of the Kuroshio Current [28N, 152E]) would result in $h_o/R = 0.33$, much lower than Huppert's (1975) critical value. Surface currents during this survey were apparently much stronger than during the first survey: in spite of decreased wind speed (by approximately a factor of 3), the speed of the ship's drift during CTD operations of the second survey was about 3 times faster than during the first survey (means [±SD] were 33.4 ± 13.7 and 12.9 ± 8.6 cm s^{-1}, respectively, subject to the unrecorded variability inherent in the ship's drift measurements). Similarly, Owens and Hogg (1980) have found that a persistent Taylor column was undetectable above a seamount during a period when the largest sustained current speed was recorded. However, different conditions of complex flow might also be responsible for the absence of the cold dome during our second survey. The previously existing cold dome was probably swept downstream, away from the seamount top, since it was not encountered in the two orthogonal transects. Several observations of abundant sub-surface small-scale eddies in the mid-ocean have been attributed to the existence of seamounts upstream (Vastano and Warren, 1976; Royer, 1978).

c. Third survey (March 30, 1984). Quasihorizontal isotherms characterized the waters shallower than the seamount top through the entire survey area (Fig. 5a). Sharp deflections of isotherms in the boundary zone around the slope, however, were clearly visible. An uplifting trend, much weaker than in the first survey, was found in the upper part of the slope (represented by the 15.5°C isotherm), and downward deflected isotherms in the lower part. Unlike the first survey, the deflections were not symmetrical around the seamount: the downwelling trend was shallower and more pronounced on the west slope. The "transition" layer on the west slope, between the 15°C and 15.5°C isotherms, was approximately 140 m shallower than that on the east slope (between 10.5°C and 11°C). The weak uplifting of the 15.5°C and 16°C isotherms, just above the seamount, was indistinguishable from the ambient isotherm fluctuations. Consequently, no local upwelling occurred and no chlorophyll enrichment was found above the seamount top (Fig. 5b).

On the other hand, all the chlorophyll profiles of this survey showed a pronounced chlorophyll maximum. "Hardness" values (mean [±SD] = 2.45 ± 0.24) were significantly higher than those in all previous profiles ($p < 0.01$, Mann-Whitney). An overall regional shoaling of the 17°C to 22°C isotherms, relative to their depths during the second survey and the control stations of the first one, might have been related to the formation of the strong DCM at all stations. Temperature—chlorophyll relationships showed that the main chlorophyll increase (relative to other surveys) occurred in the 21°C to 22°C range, i.e., about one degree cooler than the increase above the

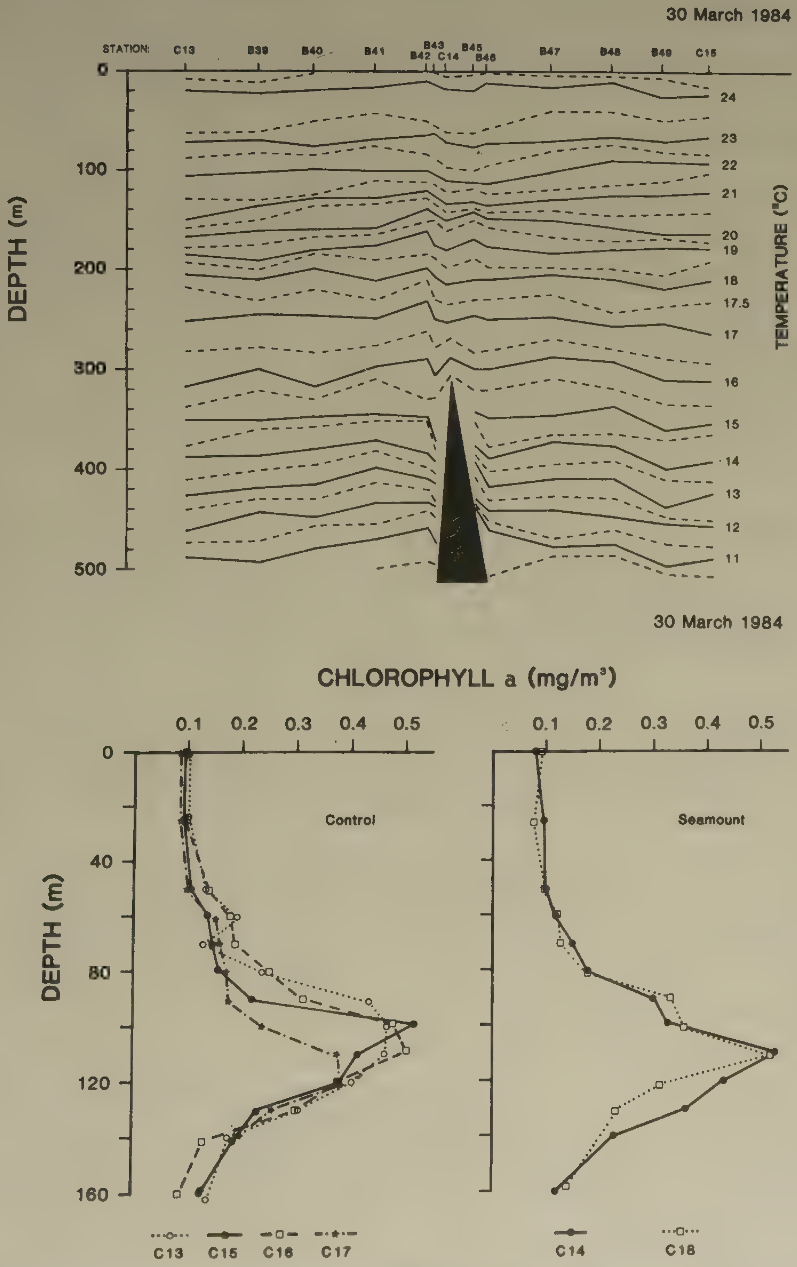

Figure 5. The third survey. (a) temperature structure along transect line AA′. Similar patterns were found along lines CC′ and DD′. (b) chlorophyll profiles above the seamount top (right) and in the control stations (left).

seamount during the first survey. We have no explanation for the cause of this regional change of the temperature structure over an area of at least 500 km^2. Zooplankton volumes in the two strata of the seamount tow were about half the quantities caught at this station during the first survey and were similar to the volumes at the control stations of both the first and third surveys (except a relatively high value at one of the control stations, Table 1).

d. The benthic boundary zone. Steplike structures along temperature profiles ("finestructures"), similar to the transition layer around the seamount slope (Fig. 2b), have been observed by Wunsch (1972) in the vicinity of Bermuda Island. The amount of finestructure increased as the island was approached, with notable asymmetry of finestructure strength around the island. Armi (1978) has found a similar multiple-step structure downstream of Corner Rise Seamount. Vertical mixing within a turbulent benthic-boundary layer has been suggested as the cause of this finestructure (Wunsch, 1972; Armi and Millard, 1976). In the presence of sloping bottom, however, reflection and breaking of internal waves can also produce mixing, finestructure, and isotherm deflections (Wunsch, 1969; Cacchione and Wunsch, 1974; Hogg *et al.,* 1978; Eriksen, 1982). Unfortunately, no current data are available to critically evaluate the actual processes which were responsible for the observed isotherm pattern within the benthic boundary zone of Minami-kasuga Seamount. This is the first field documentation of different deflection trends of isotherms in the vicinity of the bottom; more observational and theoretical work is required for a better understanding of this phenomenon. The exploration of both sediment thickness (Roberts *et al.,* 1974) and the distribution of benthic organisms on seamounts may contribute to such studies, as both variables are probably affected by such episodic events and integrate them over long periods.

e. Changes of the DCM. The seamount-induced "natural experiment" and the associated change of the chlorophyll profiles are relevant to studies of the DCM. Specifically, our observations are consistent with the hypothesis that enhanced growth of phytoplankton in the lower euphotic zone, due to nutrient replenishing from below, would contribute to the formation and maintenance of the DCM (Anderson, 1969; Venrick *et al.,* 1973; Herbland and Voituriez, 1979). Hypotheses relating the DCM to differential passive sinking of cells through irradiance and nutrient gradients (Steele and Yentsch, 1960; Bienfang, 1980), cannot explain the chlorophyll increase above the seamount since the slow sinking rate of cells (about 1 m/day or less, Bienfang, 1980) would require very long entrapment times to form this increase. Similarly, increase of the chlorophyll:carbon ratio of phytoplankton in the cold dome (Steele, 1964; Kiefer *et al.,* 1976; Bienfang *et al.,* 1983) cannot explain the observed strong DCM since increase of this ratio is expected to occur when the organisms are downwelled to a lower light regime, rather than when upwelling occurs as in the present study. The formation of sharp DCM by an increase of chlorophyll concentrations in that layer, rather than by a decrease in adjacent layers, and the higher zooplankton abundance found within the cold dome (Table 1) are inconsistent with the possibility that zooplankton grazing was responsible for the development of the sharp DCM (Longhurst, 1976, Jamart *et al.*, 1977).

5. Conclusions

Our observations suggest the existence of a highly dynamic system above the seamount. Intermittent upward deflection of isotherms can result in the formation of cold domes, similar to a Taylor column. These domes may penetrate into the euphotic zone and affect phytoplankton abundance in the overlying water. Seamounts are thereby a source of both physical and biological patchiness in the surrounding ocean, as features generated above them are swept away. Thus, relatively more finestructure in temperature profiles (Armi, 1978), higher variability (or patchiness) of chlorophyll profiles, and relatively high abundance of eddies (Vastano and Warren, 1976; Huppert and Bryan, 1976; Royer, 1978) are expected to be found downstream of seamounts. Biological effects in the euphotic layer, however, are less likely to be induced by deeper seamounts and by unsteady impinging currents.

Isotherm deflections within the benthic boundary zone also occur intermittently, even when no distinctive upwelling is generated above the seamount. These events are probably related to additional physical processes such as boundary layer mixing (Armi, 1978) or internal wave interactions with sloping bottom (Cacchione and Wunsch, 1974; Eriksen, 1982).

Our observations cannot explain the high abundance of fish over seamounts as the involved entrapment time was apparently too short for the enrichment to proceed to higher trophic levels. Nevertheless, it is possible that these events may also occur either frequently for short periods or for longer durations, thereby influencing higher trophic levels. Biological studies of interactions between a steady current such as the Kuroshio and the Emperor Seamounts, where the upwelling apparently reaches the surface (Roden and Taft, 1985) and long entrapment periods have been observed (Cheney *et al.*, 1980), are therefore highly desirable.

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REFERENCES

Anderson, G. C. 1969. Subsurface chlorophyll maximum in the northeast Pacific Ocean. Limnol. Oceanogr., *14*, 386–391.

Armi, L. 1978. Some evidence for boundary mixing in the deep ocean. J. Geophys. Res., *83,* 1971–1979.

Armi, L. and R. C. Millard, Jr. 1976. The bottom boundary layer of the deep ocean. J. Geophys. Res., *81,* 4983–4990.

Backus, R. H., G. R. Flierl, D. R. Kester, D. B. Olson, P. L. Richardson, A. C. Vastano, P. H. Wiebe and J. H. Wormuth. 1981. Gulf Stream cold-core rings: their physics, chemistry, and biology. Science, *212,* 1091–1100.

Bienfang, P. K. 1980. Phytoplankton sinking rates in oligotrophic waters off Hawaii, USA. Mar. Biol., *61,* 69–77.

Bienfang, P. K. and J. P. Szyper. 1981. Phytoplankton dynamics in the subtropical Pacific Ocean off Hawaii. Deep-Sea Res., *28,* 981–1000.

Bienfang, P. K., J. P. Szyper and E. Laws. 1983. Sinking rate and pigment responses to light-limitation of a marine diatom: implications to dynamics of chlorophyll maximum layers. Oceanol. Acta, *6,* 55–62.

Bienfang, P. K. and M. Takahashi. 1983. Ultraplankton growth rates in a subtropical ecosystem. Mar. Biol., *76,* 213–218.

Boehlert, G. W. In review. Seamount resources: hypotheses and future research directions, *in* The Environment and Resources of Seamounts in the North Pacific, R. N. Uchida and S. Hayasi, eds., NOAA Tech. Report, NMFS.

Boehlert, G. W., D. M. Gadomski and B. C. Mundy. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull., U.S., *83,* (in press).

Boehlert, G. W. and M. P. Seki. 1984. Enhanced micronekton abundance over mid-Pacific seamounts. EOS, Trans. Am. Geophys. Union, *65,* 928. [Abstract].

Cacchione, D. and C. Wunsch. 1974. Experimental study of internal waves over a slope. J. Fluid Mech., *66,* 223–239.

Cheney, R. E., P. L. Richardson and K. Nagasaka. 1980. Tracking a Kuroshio cold ring with a free-drifting surface buoy. Deep-Sea Res., *27,* 641–654.

Connell, J. H. 1974. Ecology: field experiments in marine ecology, *in* Experimental Marine Biology, Academic Press, New York, 21–54.

Cullen, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a.* Can. J. Fish. Aquat. Sci., *39,* 791–803.

Dandonneau, Y. 1979. Concentrations en chlorophylle dans le Pacifique tropical sud-ouest: comparaison avec d'autres aires oceaniques tropicales. Oceanol. Acta, *2,* 133–142.

Dayton, P. K. and J. S. Oliver. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments, *in* Marine Benthic Dynamics, K. R. Tenore and B. C. Coull, eds., University of South Carolina Press, Columbia, 93–120.

Eide, L. I. 1979. Evidence of a topographically trapped vortex on the Norwegian continental shelf. Deep-Sea Res., *26,* 601–621.

Emery, W. J. and J. S. Dewar. 1982. Mean temperature-salinity, salinity-depth and temperature-depth curves for the North Atlantic and North Pacific. Prog. Oceanogr., *11,* 219–305.

Eppley, R. W. 1981. Relations between nutrient assimilation and growth in phytoplankton with a brief review of estimates of growth rate in the ocean. Can. Bull. Fish. Aquat. Sci., *210,* 251–263.

——1982. The PRPOOS program: a study of plankton rate processes in oligotrophic oceans. EOS, Trans. Am. Geophys. Union, *163,* 522.

Eriksen, C. C. 1982. Observations of internal wave reflection off sloping bottoms. J. Geophys. Res., *87,* 525–538.

Fukasawa, M. and Y. Nagata. 1978. Detailed oceanic structure in the vicinity of the shoal Kokusho-sone. J. Oceanogr. Soc. Japan, *34,* 41–49.

Furnas, M. J. 1982. Growth rates of summer nanoplankton (<10 μm) populations in lower Narragansett Bay, Rhode Island, USA. Mar. Biol., *70,* 105–115.

Goldman, J. C., J. J. McCarthy and D. G. Peavey. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature, *279,* 210–215.

Gould, W. J., R. Hendry and H. E. Huppert. 1981. An abyssal topographic experiment. Deep-Sea Res., *28,* 409–440.

Herbland, A. and B. Voituriez. 1979. Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean. J. Mar. Res., *37,* 87–101.

Herlinveaux, R. H. 1971. Oceanographic features of and biological observations at Bowie Seamount, 14–15 August, 1969. Fish. Res. Board Can., Tech. Rep., *273.*

Hogg, N. G. 1973. On the stratified Taylor column. J. Fluid Mech., *58,* 517–537.

Hogg, N. G., E. J. Katz and T. B. Sanford. 1978. Eddies, islands, and mixing. J. Geophys. Res., *83,* 2921–2938.

Hokkaido University. 1967. Data record of oceanographic observations and exploratory fishing. The Faculty of Fisheries, Hokkaido University, *11,* 1–119.

—— 1968. Data record of oceanographic observations and exploratory fishing. The Faculty of Fisheries, Hokkaido University, *12,* 29–113.

—— 1969. Data record of oceanographic observations and exploratory fishing. The Faculty of Fisheries, Hokkaido University, *13,* 231–308.

Holm-Hansen, O., C. J. Lorenzen, R. W. Holmes and J. D. H. Strickland. 1965. Fluorometric determination of chlorophyll. J. Cons. Perm. Int. Explor. Mer, *30,* 3–15.

Hubbs, C. L. 1959. Initial discoveries on fish faunas on seamounts and offshore banks in the eastern Pacific. Pac. Sci., *13,* 311–316.

Hughes, S. E. 1981. Initial U.S. exploration of nine Gulf of Alaska seamounts and their associated fish and shellfish resources. Mar. Fish. Rev., *43,* 26–33.

Huppert, H. E. 1975. Some remarks on the initiation of internal Taylor columns. J. Fluid Mech., *67,* 397–412.

Huppert, H. E. and K. Bryan. 1976. Topographically generated eddies. Deep-Sea Res., *23,* 655–679.

Hussong, D. M. and P. Fryer. 1983. Back-arc seamounts and the SeaMARC II seafloor mapping system. EOS, Trans. Am. Geophys. Union, *64,* 627–632.

Jackson, G. A. 1980. Phytoplankton growth and zooplankton grazing in oligotrophic oceans. Nature, *284,* 439–441.

Jamart, B. M., D. F. Winter, K. Banse, G. C. Anderson and R. K. Lam. 1977. A theoretical study of phytoplankton growth and nutrient distribution in the Pacific Ocean off the northwestern U.S. coast. Deep-Sea Res., *24,* 753–773.

Japan Oceanographic Data Center. 1977–1979. Data Report of CSK. Hydrographic Department, Maritime Safety Agency, Tokyo, *385, 395, 406, 415, 424, 430, 439.*

Kiefer, D. A., R. J. Olson and O. Holm-Hansen. 1976. Another look at the nitrite and chlorophyll maxima in the central North Pacific. Deep-Sea Res., *23,* 1199–1208.

Laws, E. A., D. G. Redalje, L. W. Haas, P. K. Bienfang, R. W. Eppley, W. G. Harrison, D. M. Karl and J. Marra. 1984. High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. Limnol. Oceanogr., *29,* 1161–1169.

Longhurst, A. R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Res., *23,* 729–754.

McGowan, J. A. and P. W. Walker. 1979. Structure in the copepod community of the North Pacific central gyre. Ecol. Monogr., *49,* 195–226.

Meincke, J. 1971. Observation of an anticyclonic vortex trapped above a seamount. J. Geophys. Res., *76,* 7432–7440.

Olson, D. B. and R. H. Backus. 1985. The concentrating of organisms at fronts: a cold-water fish and a warm-core Gulf Stream ring. J. Mar. Res., *43*, 113–137.

Owens, W. B. and N. G. Hogg. 1980. Oceanic observations of stratified Taylor columns near a bump. Deep-Sea Res., *27*, 1029–1045.

Redalje, D. G. and E. A. Laws. 1981. A new method for estimating phytoplankton growth rates and carbon biomass. Mar. Biol., *62*, 73–79.

Richardson, P. L. 1980. Anticyclonic eddies generated near the Corner Rise seamounts. J. Mar. Res., *38*, 673–686.

Roberts, D. G., N. G. Hogg, D. G. Bishop and C. G. Flewellen. 1974. Sediment distribution around moated seamounts in the Rockall Trough. Deep-Sea Res., *21*, 175–184.

Roden, G. I. and B. A. Taft. 1985. Effect of the Emperor Seamounts on the mesoscale thermohaline structure during the summer of 1982. J. Geophys. Res., *90*, 839–855.

Royer, T. C. 1978. Ocean eddies generated by seamounts in the North Pacific. Science, *199*, 1063–1064.

Schmitz, W. J., Jr., P. P. Niiler, R. L. Bernstein and W. R. Holland. 1982. Recent long-term moored instrument observations in the western North Pacific. J. Geophys. Res., *87*, 9425–9440.

Steele, J. H. 1964. A study of production in the Gulf of Mexico. J. Mar. Res., *22*, 211–222.

—— 1977. (Ed.) Spatial Pattern in Plankton Communities. Plenum, New York, 470 pp.

Steele, J. H. and C. S. Yentsch. 1960. The vertical distribution of chlorophyll. J. Mar. Biol. Assoc. U. K., *39*, 217–226.

Taylor, G. I. 1923. Experiments on the motion of solid bodies in rotating fluids. Roy. Soc. Lond. Proc., *104A*, 213–218.

Thomas, W. H. 1970. Effect of ammonium and nitrate concentration on chlorophyll increases in natural tropical Pacific phytoplankton populations. Limnol. Oceanogr., *15*, 386–394.

Uchida, R. N. and D. T. Tagami. 1984. Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. Mar. Fish. Rev., *46*(2), 1–17.

Uda, M. and M. Ishino. 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. J. Tokyo Univ. Fish., *44*, 105–119.

Vastano, A. C. and B. A. Warren. 1976. Perturbations to the Gulf Stream by Atlantis II Seamount. Deep-Sea Res., *23*, 681–694.

Venrick, E. L., J. A. McGowan and A. W. Mantyla. 1973. Deep maxima of photosynthetic chlorophyll in the Pacific Ocean. Fish. Bull., U.S., *71*, 41–52.

Welschmeyer, N. A. and C. J. Lorenzen. 1985. Chlorophyll budgets: zooplankton grazing and phytoplankton growth in a temperate fjord and the central Pacific gyres. Limnol. Oceanogr., *30*, 1–21.

Wunsch, C. 1969. Progressive internal waves on slopes. J. Fluid Mech., *35*, 131–144.

—— 1972. Temperature microstructure on the Bermuda slope with application to the mean flow. Tellus, *24*, 350–367.

Yentsch, C. S. and D. W. Menzel. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res., *10*, 221–231.

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CONFIDENCE LIMITS FOR POPULATION PROJECTIONS WHEN VITAL RATES VARY RANDOMLY

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ABSTRACT

Due to unpredictable future environmental changes, population growth is more realistically viewed as a stochastic than a deterministic process. Environmental variablity is modeled by allowing the population's survival and fecundity rates to be correlated random variables. The expected future population vector and its variance-covariance matrix are computed. The projected total future population size is approximately lognormally distributed, but confidence limits for future population size can be more accurately computed from the distribution of the realized factor of increase. Numerical examples illustrate how the calculation of confidence limits for future population size and of the probability that the population will increase in size can be applied to the management of living resources.

The predicted size of an age-structured population can be projected if its initial size, age distribution, and vital rates are known (e.g., Leslie 1945; Keyfitz 1968). Such population projections are commonly used in fisheries and wildlife management when age-specific fecundity and mortality rates are available. However, there is uncertainty in such projections. First, we rarely know vital rates exactly; rather, we have estimates of the true rates, and these estimates are subject to sampling and other types of errors. Second, the true rates themselves are not constant with time. Environmental conditions are always changing, and the vital rates would be expected to change in response. To an extent, the changes of conditions may themselves be forecast and incorporated into a population model. Some changes, however, are unpredictable, and these changes give rise to fluctuations in the vital rates which make our estimates of population size for some future time less certain. Nevertheless, it may still be possible to make probabilistic predictions about future population size given some statistical knowledge about the fluctuating vital rates.

In this paper we limit ourselves to consideration of the second of these problems, projecting age-structured populations when mortality and fecundity rates vary randomly with time. Recently this topic has been of interest and controversy in a more theoretical context (Boyce 1977; Cohen 1979a, b; Daley 1979; Tuljapurkar and Orzack 1980; Tuljapurkar 1982; Slade and Levenson 1982). In spite of earlier results to the contrary (Boyce 1977), analyses (Sykes 1969; Cohen 1977), and simulations (Slade and Levenson 1982) have shown that when vital rates fluctuate randomly with no serial correlation, the expectation of population size at a future time will be exactly equal to the population size projected using the mean vital rates in a deterministic projection. For application in fisheries and wildlife management, the problem is that the distribution of future population sizes will often be strongly skewed. This skew means that the mean and variance of future population size, even if known, are not sufficient to characterize the distribution and, in particular, not sufficient to compute confidence limits for total population size. In this paper we examine two transformations of this skewed distribution which approximate a normal distribution, and evaluate the accuracy of confidence limits computed from these transformations.

As pointed out by several of the authors cited above and earlier by Lewontin and Cohen (1969) for a non-age-structured population, stochastic effects can cause the modal or most likely population trajectory to decline to extinction, even though the expected or mean population size is growing at a geometric rate. Clearly, if we are to use population projections in fisheries and wildlife management, we should be concerned about the effects of natural variability on the results of our projections. In response to this concern, we have written two com-

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puter programs for stochastic population projections which can serve as research and management tools. Here we illustrate the utility of these programs with numerical examples, compare our results with recent theoretical analyses, and discuss the implications of these results to the management of living resources.

METHODS

Sykes (1969) presented three models for incorporating stochasticity into population projections. He concluded that the observed variability in human demographic projections was best described by his third model, in which the elements of the Leslie matrix (the effective fecundity rates and the survival rates) are random variables, each with a specified mean and variance, and with specified covariances between them. The model does not allow for serial covariance in vital rates between successive time periods.

Let $\boldsymbol{n}_t$ be a population vector of ω age classes at time t. The stochastic projection model is

$$\boldsymbol{n}_{t+1} = (\boldsymbol{A} + \boldsymbol{\Delta}_t)\, \boldsymbol{n}_t, \qquad t = 0, 1, 2, \ldots$$

where $\boldsymbol{A}$ is a constant projection matrix of mean vital rates and $\boldsymbol{\Delta}_t$ is a matrix of random deviations whose elements have a specified covariance structure $\{\mathrm{Cov}(\Delta_i, \Delta_j)\}$ but which are uncorrelated in time. Let $N_t = \sum_{i=1}^{\omega} n_{ti}$ be the total population size at time t. It is convenient to normalize the projected population to the initial population size and consider the distribution of the ratio N_t/N_0. The mean and variance of this ratio are given by

$$E(N_t/N_0) = E(N_t)/N_0$$

$$= \sum_{i=1}^{\omega} E(n_{ti})/N_0$$

and

$$\mathrm{Var}\,(N_t/N_0) = \mathrm{Var}\,(N_t)/N_0^2$$

$$= \sum_{i=1}^{\omega} \sum_{j=1}^{\omega} \mathrm{Cov}\,(n_{ti}, n_{tj})/N_0^2.$$

From Sykes (1969, equations 19 and 20), the mean and variance of the population vector are given by

$$E(\boldsymbol{n}_t) = \{E(n_{ti})\} = \boldsymbol{A}^t \boldsymbol{n}_0$$

and

$$\mathrm{Var}\,(\boldsymbol{n}_t) = \{\mathrm{Cov}\,(n_{ti}, n_{tj})\}$$

$$= \sum_{k=0}^{t-1} \boldsymbol{A}^{t-1-k} \left\{ \sum_{\alpha=1}^{\omega} \sum_{\beta=1}^{\omega} \mathrm{Cov}\,(\Delta_{i\alpha}, \Delta_{j\beta}) \right.$$

$$\left. [\mathrm{Cov}\,(n_{k\alpha}, n_{k\beta}) + E(n_{k\alpha})E(n_{k\beta})] \right\} \quad \boldsymbol{A}'^{\,t-1-k}$$

where $\boldsymbol{A}'$ is the transpose of $\boldsymbol{A}$ and where the curly brackets indicate that the expression inside them is the ith element of the vector or the ijth element of the matrix considered.

Tuljapurkar and Orzack (1980) predict that for large t, N_t/N_0 will be lognormally distributed. The mean and variance of the normally distributed variable $\log\,(N_t/N_0)$ are calculated from the mean and variance of the lognormally distributed variable N_t/N_0 by

$$E\,[\log(N_t/N_0)] = \log[E(N_t/N_0)] - \left\{ \frac{\mathrm{Var}\,[\log\,(N_t/N_0)]}{2} \right\}$$

and

$$\mathrm{Var}\,[\log\,(N_t/N_0)] = \log \left\{ \frac{\mathrm{Var}\,(N_t/N_0)}{[E(N_t/N_0)]^2} + 1 \right\}$$

(Aitchison and Brown 1957). We have found in simulations that the distribution of the realized factor of increase $(N_t/N_0)^{1/t}$ is approximately normal. Based on the assumption that the realized factor of increase is normally distributed, the mean and variance of $(N_t/N_0)^{1/t}$ are computed from the mean variance of N_t/N_0 by methods given in Appendices 1 and 2.

Using the formulae of Sykes (1969), the mean and variance of each age class in the future population can be computed analytically. Confidence intervals for the total population size and for the realized factor of increase, and an estimate of the probability that the future population will be larger than the starting population, are computed based on the assumption that either $\log\,(N_t/N_0)$ or $(N_t/N_0)^{1/t}$ is normally distributed.

We can also simulate the growth of an age-structured population under fluctuating environmental conditions. At each time period, a new set of fecundity and survival rates, the elements of the Leslie matrix, are chosen and used to project the population. Each fecundity and survival rate is a normally distributed random variable with specified mean, variance, and covariance with every other fecundity and survival rate. The projection, starting from the same initial population vector, may be replicated a given number of times. From these replicated projections, the mean, variance, and covariances of the population vector are computed, together with statistics on a variety of other demographic parameters. The distributions of the final population size and the realized factor of increase are tabulated.

The computer programs to accomplish these stochastic projections are called, respectively, SPP (Stochastic Population Projection) and SLT (Stochastic Life Table simulation). Program listings and guides to the use of both programs are given in Gerrodette et al. (1983). Although lengthy, these programs are suitable for use on many microcomputers.

TABLE 1.—Initial population vector, mean vital rates, and covariance matrix of vital rates for a three age-class population projection. In the covariance matrix, *F* refers to fecundity rate, *P* to survival rate, and numbers to age classes.

Age class	Initial population size	Mean fecundity rate	Mean survival rate	Covariance matrix						
					*F*1	*F*2	*F*3	*P*1	*P*2	*P*3
1	100	0.1	0.7	*F*1	0.0010	0.0020	0.0020	0.0005	0.0005	0.0
2	80	1.0	0.9	*F*2		0.0050	0.0045	0.0010	0.0010	0.0
3	50	0.4	0.0	*F*3			0.0050	0.0010	0.0010	0.0
	230			*P*1				0.0050	0.0045	0.0
				*P*2					0.0050	0.0
				*P*3						0.0

Numerical Examples

Two numerical examples are presented to verify various analytic results and to illustrate the use of programs SPP and SLT in a management context.

The first example is a simple artificial life table with three age classes. The mean vital rates and the covariance matrix for the vital rates are given in Table 1. This example was used to compare the predicted mean and variance in projected population size based on Sykes' (1969) formulae with the actual mean and variance from the simulation. The example was also used to test the assumption that ultimate population sizes will be lognormally distributed, and in particular whether accurate confidence limits for the tails of the distribution can be made based on this assumption.

The second example is based on a real population. A northern fur seal, *Callorhinus ursinus*, population is projected using vital rates consistent with a phase of rapid growth which occurred earlier in this century. The mean vital rates which govern the dynamics of the population are given in Table 2 (taken from Goodman 1981: table 1) and confer a population growth rate of about 8% per year. The initial age vector in this case was chosen to be the stable age distribution with a total of 100,000 females. Values for the standard deviations in vital rates in Table 2 were selected by choosing reasonable values for their coefficients of variation. Correlations in vital rates were assumed to be 0.9 between fecundities at different ages, 0.9 between survival rates at different ages, and 0.5 between all fecundities and survival rates.

TABLE 2.—Initial population vector, means, and standard deviations (S.D.) of vital rates for a fur seal population projection used as a numerical example in the text. Mean rates are taken from Goodman (1981: table 1). Each age class represents 1 yr, and only the female portion of the population is tabulated. The initial population vector is in the stable age distribution with a total of 100,000 females.

Age class	Initial population size	Mean fecundity rate	S.D.	Mean survival rate	S.D.
1	17,618	0.0000	0.0000	0.8786	0.0439
2	14,312	0.0000	0.0000	0.8786	0.0439
3	11,627	0.0050	0.0003	0.8837	0.0442
4	9,500	0.0151	0.0008	0.8888	0.0444
5	7,807	0.2631	0.0132	0.9039	0.0090
6	6,525	0.3693	0.0185	0.9191	0.0092
7	5,545	0.4250	0.0213	0.9342	0.0093
8	4,789	0.4604	0.0230	0.9443	0.0094
9	4,182	0.4756	0.0238	0.9494	0.0095
10	3,671	0.4705	0.0235	0.9443	0.0094
11	3,205	0.4655	0.0233	0.9292	0.0093
12	2,753	0.4554	0.0228	0.9039	0.0090
13	2,301	0.4402	0.0220	0.8786	0.0088
14	1,869	0.4250	0.0213	0.8484	0.0085
15	1,466	0.4048	0.0202	0.8029	0.0080
16	1,089	0.3794	0.0190	0.7524	0.0075
17	757	0.3542	0.0177	0.6918	0.0069
18	484	0.3187	0.0159	0.6262	0.0063
19	280	0.2833	0.0142	0.5454	0.0055
20	141	0.2479	0.0124	0.4494	0.0045
21	59	0.2024	0.0101	0.3282	0.0033
22	18	0.1467	0.0073	0.1009	0.0010
23	2	0.0657	0.0033	0.0000	0.0000
Total	100,000				

RESULTS

Example 1.

The results of the stochastic projection by program SPP are presented in Table 3. The second column shows the expected (mean) population vector for each time step. The mean population vector is obtained by projecting with the mean vital rates. The covariance matrix for the population vector gives, on the diagonal, the variances of each age class and, above the diagonal, the covariances between age classes.

The calculations using Sykes' formulae concur with the results of the Monte Carlo simulation of a stochastic population projection, taking the entries of the life table as time-varying random variables (program SLT). In Tables 4 and 5 the results of the simulation are presented. The means and covariances of the vital rates actually achieved on this particular run of program SLT are shown in Table 4 and are close to the specified rates given in Table 1. By comparing the results in Table 5 with those of time step 6 in Table 3, we see that the results of the simulation (SLT) and the analytic solution (SPP) agree closely.

The distribution of the ratio of the final population size to the initial population size is shown as a histogram in Figure 1A. The curve is skewed to the right,

TABLE 3.—Results of the stochastic projection of the population, given in Table 1, through 6 time steps (program SPP). The columns labeled "95% C.L." give the lower and upper 95% confidence limits for total population size and for the realized factor of increase relative to the initial population. The last column gives the probability *P* that the final population size will be greater than the initial population size.

Time step	Expected population vector	Covariance matrix			Total population Mean	Total population Lower 95% C.L. Upper 95% C.L.	Factor of increase Mean	Factor of increase Lower 95% C.L. Upper 95% C.L.	*P*
0	100				230				
	80								
	50								
1	110	142.5	18.0	14.4	252	215	1.096	0.934	0.8764
	70		50.0	36.0		289		1.258	
	72			32.0					
2	110	261.5	48.4	73.5	250	197	1.041	0.925	0.7545
	77		131.0	46.1		307		1.156	
	63			65.3					
3	113	365.3	94.4	154.1	259	193	1.039	0.934	0.7856
	77		189.7	68.7		335		1.134	
	69			136.4					
4	116	485.5	158.2	219.9	264	187	1.033	0.950	0.7808
	79		244.9	99.0		356		1.116	
	69			184.2					
5	119	559.6	230.8	287.1	271	184	1.031	0.957	0.7910
	81		307.5	141.7		378		1.105	
	71			231.0					
6	121	736.2	309.8	366.2	277	182	1.029	0.961	0.7990
	83		367.0	189.7		400		1.096	
	73			283.5					

TABLE 4.—Means, variances, and covariances of vital rates achieved during a Monte Carlo projection of the population given in Table 1 (program SLT). Values were computed on the basis of 30,000 vectors of vital rates. *F* refers to fecundity rate, *P* to survival rate, and numbers to age classes. Values in this table should be compared with the "target" values in Table 1.

	Mean	Covariance matrix *F*1	*F*2	*F*3	*P*1	*P*2	*P*3
*F*1	0.10016	0.00101	0.00202	0.00201	0.00049	0.00045	0.0000
*F*2	1.00027		0.00505	0.00453	0.00100	0.00092	0.0000
*F*3	0.39998			0.00502	0.00099	0.00091	0.0000
*P*1	0.69992				0.00501	0.00414	0.0000
*P*2	0.89744					0.00435	0.0000
*P*3	0.00000						0.0000

TABLE 5.—Results of the Monte Carlo simulation of the 6 time-step projection of the population whose age structure and vital rates are given in Table 1 (program SLT). Sample size for the simulation was 5,000 trials. Results in this table should be compared with the "predicted" values in the last row of Table 3. Here P is the proportion of final population sizes greater than the initial population size.

Time step	Mean population vector	Covariance matrix			Mean total population	Mean factor of increase	P
	121	741.3	314.7	369.8			
6	83		371.7	187.6	277	1.029	0.7954
	73			281.5			

as anticipated. Both the logarithmic transformation (Fig. 1B) and the root transformation (Fig. 1C) appear to normalize the distribution. When the cumulative frequency distributions are plotted on normal probability scales (dots in Fig. 1), however, the root transformation appears superior to the logarithmic. The dots in Figure 1C are nearly linear, indicating that the distribution is close to normal.

In Table 6 the accuracy of the 95% confidence limits for the total population size computed by the logarithmic and root transformations is compared for projections of 2, 5, and 10 time steps, using the same numerical example. Program SLT calculates the proportion of final populations which fall above and below the computed upper and lower confidence limits. We expect that 2.5% of the cases should fall above the upper limit and 2.5% below the lower limit if the 95% confidence interval has been correctly estimated. Table 6 shows that both the logarithmic and the root transformations do a fair job of estimating the 95% confidence limits. The root transformation, however, appears more accurate in this example, as well as in other examples we have tried, when the number of time steps is small. When the number of time steps is large (50-100), both transformations produce normally distributed variables.

Since the root transformation gave the most accurate results for short projections, we used this transformation in program SPP to compute a confidence interval on total population size. More details of the

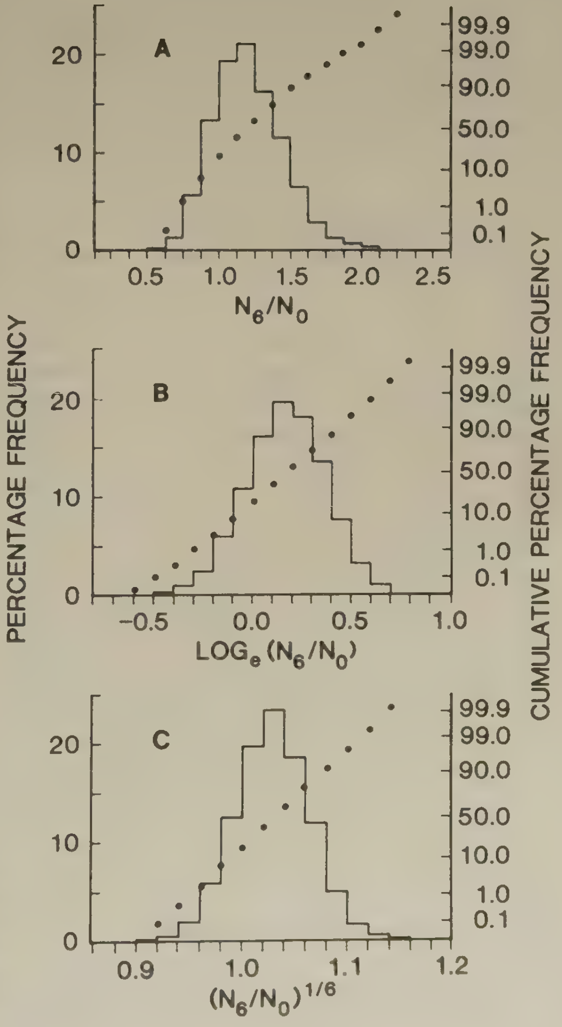

FIGURE 1.—Distributions of future total population size under variable conditions. Histograms show the percentage frequency, and dots the cumulative percentage frequency plotted on a normal probability scale, for 5,000 stochastic projections of the population given in Table 1 for six time steps. A. Distribution of N_6/N_0, the final population size divided by the initial. B. Distribution of $\log_e (N_6/N_0)$. C. Distribution of $(N_6/N_0)^{1/6}$, the realized factor of increase.

TABLE 6.—Accuracy of the 95% confidence limits (C.L.) on population size estimated by the logarithmic and root transformations of the distribution of total population size. For each transformation, the estimated lower and upper confidence limits are shown for projections of the population given in Table 1 for 2, 5, and 10 time steps. The columns labeled "Proportion beyond C.L." give the actual proportion of 10,000 stochastic projections using program SLT which fall below the estimated lower limit and above the estimated upper limit for each transformation. Each set of projections was replicated 3 times. The root transformation estimates the 95% confidence interval on population size more accurately, especially for short projections.

No. of time steps to projection		Transformation			
		Logarithmic		Root	
		Estimated 95% C.L.	Proportion beyond C.L.	Estimated 95% C.L.	Proportion beyond C.L.
2	Lower	199	0.0311	197	0.0256
			0.0317		0.0255
			0.0295		0.0231
	Upper	309	0.0160	307	0.0204
			0.0181		0.0214
			0.0199		0.0228
5	Lower	187	0.0290	184	0.0251
			0.0285		0.0242
			0.0318		0.0260
	Upper	380	0.0227	378	0.0245
			0.0219		0.0235
			0.0215		0.0235
10	Lower	178	0.0266	175	0.0238
			0.0280		0.0252
			0.0286		0.0257
	Upper	489	0.0226	486	0.0234
			0.0211		0.0221
			0.0217		0.0226

example projection are shown in the columns on the right side of Table 3. The mean and the 95% confidence interval for the total population size and for the realized factor of increase are given for each time step. As the population vector approaches the stable age distribution, the ratio between successive mean total population sizes approaches the asymptotic value 1.0240. The mean realized factor of increase shown in Table 3, which is computed relative to the initial population, does not converge on this asymptotic value; nor can the mean realized factor of increase be computed from the ratio of the mean final population size to the initial population size. Instead, the mean and variance of the realized factor of increase are computed by methods described above.

The probability that the total population size will have increased over its initial value is also shown for each time step in the last column of Table 3. In this particular example, since we did not begin with the stable age distribution, this probability decreases at first and then increases. As a further check, program SLT computes the proportion of cases in which the final population was greater than the initial population, and this answer (0.7954, Table 5) is close to the probability computed analytically by program SPP assuming that the realized factor of increase is normally distributed (0.7990, Table 3). Given a population whose age structure and dynamics conform to the values given in Table 1, therefore, we can make the statement that there is an 80% chance that the population will be larger 6 time steps from now and a 20% chance that it will be smaller.

Example 2.

The results of the stochastic projection of the northern fur seal population by program SPP are given in Table 7 and Figure 2. Table 7 shows that after 5 yr, the expected (mean) number of 9-yr-olds, for example, is 6,188 with a standard deviation of 333. The expected total population size is 147,982 with a standard deviation of 8,832. The mean and standard deviation of the realized factor of increase are 1.0812 and 0.0129, respectively; from these values we compute the 99% confidence interval on population size to be from 126,410 to 171,930. Note

TABLE 7.—Results of the 5-yr stochastic projection of the northern fur seal population, based on the age structure and vital rates given in Table 2. Probability that the final population > initial population = 0.999+.

Age class	Expected population size	Standard deviation
1	26,071	1,672
2	21,179	1,619
3	17,205	1,519
4	14,058	1,402
5	11,553	1,280
6	9,655	972
7	8,205	720
8	7,087	516
9	6,188	333
10	5,432	121
11	4,743	106
12	4,075	92
13	3,406	76
14	2,767	62
15	2,170	49
16	1,611	36
17	1,121	25
18	717	16
19	415	9
20	209	5
21	87	2
22	26	1
23	2	0.05
Total	147,982	

	Total population	Factor of increase
Lower 99% C.L.	126,410	1.0480
Expected value (mean)	147,982	1.0812
Upper 99% C.L.	171,930	1.1145

that, as will generally be the case, the confidence interval for total population size is not symmetric about the mean value.

In the last line of Table 7, the probability of an increased population is shown to be very close to 1.0. In other words, it is virtually certain that the population will have increased in size after 5 yr. Figure 2 presents the results for total population size graphically. The 95% and 99% confidence limits computed by program SPP are shown for each time step. The confidence limits grow nearly geometrically.

DISCUSSION

Fishery and wildlife management often involves predictions of population size, and, owing to imperfect knowledge of the world, these predictions are uncertain. Accordingly, a practical analysis attaches estimates of confidence intervals for any given prediction. The programs described in this paper carry out the computation of confidence intervals for projections of age-structured populations, if we can specify the statistics of the variation in the age-specific vital rates. Realistically, we do not expect there to be be many examples where the statistics of the variation in vital rates are genuinely known with substantial precision, for these rates are difficult to measure in natural populations. Nevertheless, in an imperfect world, management decisions must be made with imperfect data. A considerable component of the uncertainty in a population prediction will be owing to the phenomena treated in this paper. Thus, even the use of very rough guesses at the statistics of the variation in the age-specific vital rates, in order to estimate confidence intervals in a population projection, is preferable to neglecting this source of variation entirely. At the very least, incorporation of speculative estimates in this applied context will allow the exploration of "what if" questions in a fashion that can indicate priorities for future data gathering.

In many fish and aquatic invertebrate species, there is an enormous variation in the success of year classes. In such cases the population dynamics may be dominated by the overwhelming abundance of one

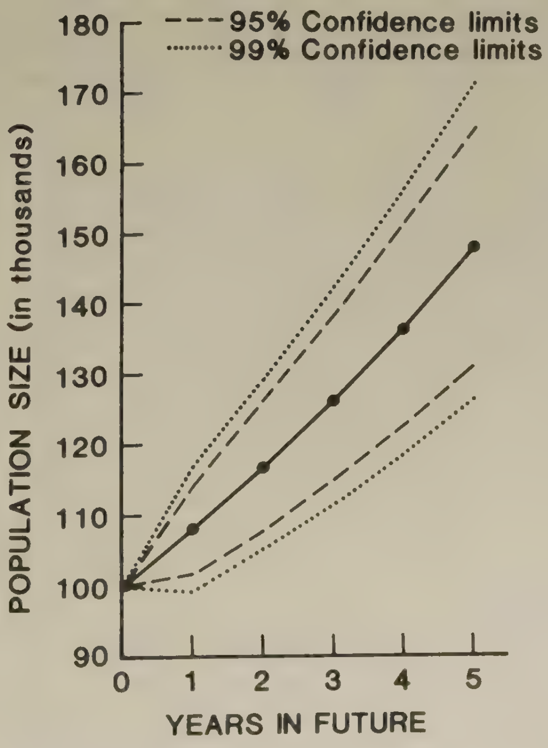

FIGURE 2.–Confidence limits for future total female population size for the northern fur seal, based on the schedule of vital rates in Table 2. The solid line plots the mean population trajectory.

or two cohorts. The environmental factors which lead to such huge variations in recruitment are as yet imperfectly understood for most species. In order to predict future population sizes, the year-to-year variation could be incorporated into the variances of the effective fecundity terms in the first row of the Leslie matrix. This will lead to enormous (but realistic) confidence limits for predicted future population sizes of such stocks. A more fruitful use of the results of this paper, however, would be to separate recruitment uncertainty from survival uncertainty and to calculate a confidence interval on future population size given recruitment success for a particular cohort. Among harvested species such a conditional forecast could be used to incorporate environmental variation into management recommendations.

In keeping with the fact that applied management may often depend on very elementary quantities, we also calculate a particularly important special statistic of the distribution of projections – the probability that the population will increase under the specified conditions. In the first example, the probability of an increased population was found to be about 0.8. In the second example, the fur seal population projection, there is a higher probability that the population will increase. Starting with the female population of 100,000, the calculations indicate 99% certainty that the population will have increased to between 126,410 and 171,930 in 5 yr.

Our simulations of stochastic population growth differ from previous efforts by Boyce (1977) and Slade and Levenson (1982) by allowing all vital rates to vary simultaneously, rather than only one at a time, and by permitting correlations among the vital rates to be specified. In the stochastic growth models of Cohen (1977, 1979a) and Tuljapurkar and Orzack (1980), at each time step the population finds itself in one of several possible environments. Within each environment vital rates are fixed. By contrast, here we model a single variable environment whose conditions, as reflected in the population's vital rates at any point in time, are never precisely duplicated. The results of Example 1 verify the results for the mean and variance of future population vectors and show that the mean and variance for total ultimate population size can be computed from Sykes' formulae. Our results confirm the conclusions of Cohen (1977), Tuljapurkar and Orzack (1980), and Slade and Levenson (1982) that the expected mean value of a stochastic population projection with no serial correlation in vital rates is equivalent to the value projected deterministically from mean vital rates. Cohen (1979a, b) and Tuljapurkar (1982) address the more general question of serial correlation in vital rates.

All of the work cited above has been concerned with the state of the population at a time in the future much greater than will generally be useful in management. In this paper we have examined the stochastic behavior of the population at a shorter time in the future. Example 1 has verified that the distribution of ultimate population sizes from stochastic population projections is approximately lognormal (Tuljapurkar and Orzack 1980). From the perspective of fitting the tails of this distribution for a small number of time steps t, however, it appears better to assume that the $1/t$th power of the distribution is normally distributed. In either case the distribution of ultimate population sizes is skewed (with long tails at the higher values), and the skew becomes more pronounced as t increases. An important property of such a distribution is that the most likely or modal population value will always be smaller than the mean. How much smaller depends on the number of time steps t, and on the variances and covariances among the survival and fecundity rates.

An interesting theoretical and practical problem is to find a descriptor of population growth under stochastic conditions which characterizes the skewed distribution of ultimate population size. Cohen (1979a) has proposed two measures of long-run population growth: λ, the ensemble average of realized factors of increase; and μ, the factor of increase needed to realize the ensemble average of final population sizes. The first is a measure based on growth rates, while the second is based on population sizes (Cohen 1979b). The average realized factor of increase calculated here is analogous to λ. If the Leslie matrix of mean vital rates is known, μ is easily calculated as the dominant eigenvalue of that matrix. The problem, as we have seen, is that under stochastic conditions the mean of the population sizes is not very informative and may, in fact, be misleading. Tuljapurkar (1982) has proposed a growth measure α which leads to the approximate median population size. The two measures proposed here – namely, $E[(N_t/N_0)^{1/t}]$ and $E[\log(N_t/N_0)]$ – are close approximations to the rate of growth leading to the modal population size. As such, they may loosely be said to describe the most probable trajectory of the population under stochastic conditions.

ACKNOWLEDGMENTS

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LITERATURE CITED

AITCHISON, J., AND J. A. C. BROWN.
1957. The lognormal distribution with special reference to its uses in economics. Cambridge Univ. Press, Cambridge, 176 p.

BOYCE, M. S.
1977. Population growth with stochastic fluctuations in the life table. Theor. Pop. Biol. 12:366-373.

COHEN, J. E.
1977. Ergodicity of age structure in populations with Markovian vital rates, III: Finite-state moments and growth rate; an illustration. Adv. Appl. Prob. 9:462-475.
1979a. Long-run growth rates of discrete multiplicative processes in Markovian environments. J. Math. Anal. Appl. 69:243-251.
1979b. Comparative statics and stochastic dynamics of age-structured populations. Theor. Pop. Biol. 16:159-171.

DALEY, D. J.
1979. Bias in estimating the Malthusian parameters for Leslie matrices. Theor. Pop. Biol. 15:257-263.

GERRODETTE, T., D. GOODMAN, AND J. BARLOW.
1983. Two computer programs to project populations with time-varying vital rates. Natl. Mar. Fish. Serv. Tech. Memo. NOAA-TM-NMFS-SWFC-28, 56 p. (Copies are available through NTIS or from the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.)

GOODMAN, D.
1981. Life history analysis of large animals. *In* C. W. Fowler and T. D. Smith (editors), Dynamics of large mammal populations, p. 415-436. Wiley, N.Y.

KEYFITZ, N.
1968. Introduction to the mathematics of population. Addison-Wesley, Reading, Mass., 450 p.

LESLIE, P. H.
1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

LEWONTIN, R. C., AND D. COHEN.
1969. On population growth in a randomly varying environment. Proc. Natl. Acad. Sci. (U.S.) 62:1056-1060.

SLADE, N. A., AND H. LEVENSON.
1982. Estimating population growth rates from stochastic Leslie matrices. Theor. Pop. Biol. 22:299-308.

SYKES, Z. M.
1969. Some stochastic versions of the matrix model for population dynamics. J. Am. Stat. Assn. 64:111-130.

TULJAPURKAR, S. D.
1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. Theor. Pop. Biol. 21:114-140.

TULJAPURKAR, S. D., AND S. H. ORZACK.
1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. Theor. Pop. Biol. 18:314-342.

APPENDIX 1.

Calculation of the mean and variance of the realized factor of increase, assuming it is normally distributed.

Let λ, the realized factor of increase, be defined as the tth root of the ratio of the population size at time t to the initial population size:

$$\lambda = \left(\frac{N_t}{N_0}\right)^{1/t}$$

or

$$\lambda^t = \frac{N_t}{N_0}$$

Let μ be the mean and ν the variance of λ. The mean and variance of λ^t are given by formulae in the Methods section. The problem is to find the mean and variance of λ.

Let $F(\mu,\nu)$ be a function which gives the tth moment of λ:

$$F(\mu,\nu) = E(\lambda^t).$$

Similarly let $G(\mu,\nu)$ be a function which gives the variance of λ^t in terms of the tth and $2t$th moments of λ:

$$G(\mu,\nu) = E(\lambda^{2t}) - [E(\lambda^t)]^2.$$

Now assume that λ is normally distributed. Appendix 2 gives a recursive algorithm which allows any moment of a normally distributed variate to be calculated. From the tth and $2t$th moments of λ, the functions F and G can be computed from the equations above. Generally, F and G will be tth and $2t$th order polynomials in μ and ν. Then, with F and G known, we have a system of two equations

$$\begin{aligned} F(\mu,\nu) - E(\lambda^t) &= 0 \\ G(\mu,\nu) - \mathrm{Var}(\lambda^t) &= 0 \end{aligned}$$

in two unknowns. Given initial estimates of μ and ν, a two-variable version of Newton's method, or any similar iterative technique, can be used to converge on a simultaneous solution.

APPENDIX 2.

A recursive algorithm for computing the higher order moments of the normal distribution.

The moment generating function for the normal distribution is

$$M_x(t) = e^{\mu t + \frac{vt^2}{2}}$$

where μ is the mean and v is the variance of the normal variate x. The nth moment of x is found by evaluating, at $t = 0$, the nth derivative of $M_x(t)$ with respect to t. The nth differentiation with respect to t leads to the series

$$(\mu + vt)^n M_x(t) + \ldots + A(\mu + vt)^\alpha v^\beta M_x(t) + B(\mu + vt)^{\alpha-2} v^{\beta+1} M_x(t) + \ldots,$$

which, evaluated at $t = 0$, gives

$$\mu^n + \ldots + A\mu^\alpha v^\beta + B\mu^{\alpha-2} v^{\beta+1} + \ldots,$$

where A and B are coefficients and α and β are exponents such that $\alpha + 2\beta = n$. The next [$(n + 1)$th] differentiation of the middle terms gives

$$\begin{aligned} & A(\mu + vt)^{\alpha+1} v^\beta M_x(t) + A\alpha(\mu + vt)^{\alpha-1} v^{\beta+1} M_x(t) \\ & + B(\mu + vt)^{\alpha-1} v^{\beta+1} M_x(t) + B(\alpha - 2)(\mu + vt)^{\alpha-3} v^{\beta+2} M_x(t) \\ & = \ldots + (A\alpha + B)(\mu + vt)^{\alpha-1} v^{\beta+1} M_x(t) + \ldots \end{aligned}$$

which, evaluated at $t = 0$, gives

$$\ldots + (A\alpha + B)\mu^{\alpha-1} v^{\beta+1} + \ldots .$$

Thus the coefficient of each term of the series of the $(n + 1)$th moment can be computed from the two terms in the series of the nth moment "before" and "after" it. The exponents of μ and v follow the regular pattern shown.

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Predation on Released Spiny Lobster, *Panulirus marginatus*, During Tests in the Northwestern Hawaiian Islands

REGINALD M. GOODING

ABSTRACT—In the Northwestern Hawaiian Islands fishery for spiny lobster, Panulirus marginatus, *undersized and berried lobsters must be released. Such lobsters released in the conventional way, are very vulnerable to predation by large carnivores. Field tests showed that the white ulua,* Caranx ignobilis, *was an efficient and aggressive predator on released lobsters. Another suspected predator, the galapagos shark,* Carcharhinus galapagensis, *did not prey on released lobsters. Procedures are suggested for use by commercial fishermen that should preclude serious predation on released lobsters.*

Introduction

During 1976-82, biologists of the NMFS Southwest Fisheries Center's Honolulu Laboratory engaged in an extensive survey of the fishery resources of the Northwestern Hawaiian Islands (NWHI) (Fig. 1). In the early exploratory phase of the survey, substantial populations of spiny lobster, *Panulirus marginatus*, were discovered on several of the NWHI banks (Uchida et al., 1980). Shortly thereafter, this resource became the target of a Honolulu-based trap fishery.

Recent research has been directed toward the accumulation of knowledge which will enable sound management of the spiny lobster resource in the NWHI. Data relative to seasonal and spatial distribution and abundance, population structure, growth rate, sexual maturation, and fecundity provide the basis of a Fishery Management Plan (FMP) for the lobster fishery. The FMP prohibits the retention of egg-bearing (berried) lobsters and those <7.7 cm carapace length (CL). The regulations, which went into effect in January 1983, require that such illegal lobsters caught in the U.S. Fishery Conservation Zone around the NWHI be sorted from the catch and released alive.

On lobster fishing vessels in the NWHI, the usual procedure is to

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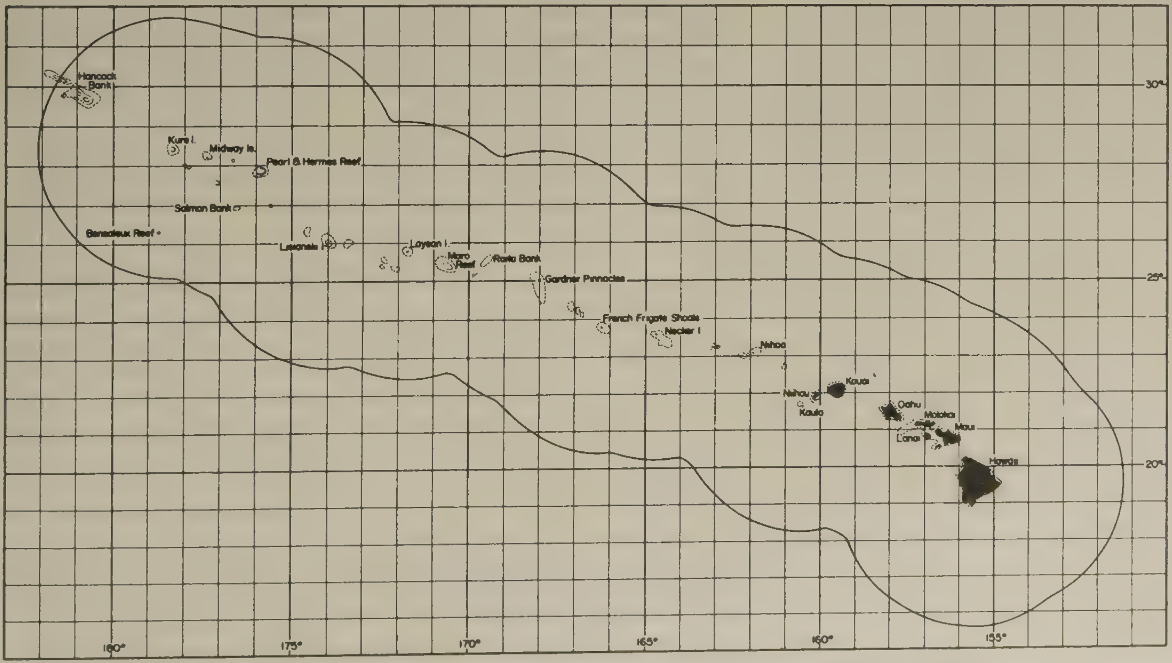
Hancock Bank
Kure I.
Midway Is.
Pearl & Hermes Reef
Salmon Bank
Bensaleux Reef
Lisianski I.
Laysan I.
Maro Reef
Raita Bank
Gardner Pinnacles
French Frigate Shoals
Necker I
Nihoa
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Hawaii
30°
25°
20°
180°
175°
170°
165°
160°
155°

Figure 1.—The Hawaiian Archipelago including the Northwestern Hawaiian Islands.

release illegal lobsters overboard immediately after traps are hauled. Concurrently, old bait remaining in the traps is also discarded. During the period the fishery was unregulated, no estimate was available of the number of lobsters which were caught and released by commercial fishermen. However, the logbook data furnished NMFS by vessels in the NWHI fishery show that for 1983, 23.2 percent of all lobsters trapped were <7.7 cm CL (legally undersized) and 4.4 percent were berried. On grounds that are intensively fished, such as those surrounding Necker Island and Maro Reef in the NWHI, it is likely that many animals are trapped and released more than once.

The survival rate of undersized lobsters after they have been released may be of considerable significance to the long-term productivity of the NWHI lobster fishery. Thus, it is of some importance to have an understanding of the factors which affect this animal's ability to survive, grow, and reproduce normally after it has been trapped and returned to the sea. With such an understanding, it can be determined whether further regulations governing the way berried and undersized lobsters are handled by commercial fishermen are needed.

Lobsters caught in traps and subsequently released are subject to factors which may cause stress or injury and result in high mortality. These broadly include: Length of time out of the water and subsequent exposure to air, sunlight, and heat; injury resulting from handling; release on an unsuitable substrate; release in an area outside its home range; general disorientation which may make the animal more vulnerable to predation; and presence of lobster predators in the vicinity of the vessel at the time of release. Davis (1981) found that fishery-related injuries inflicted on *P. argus* resulted in a significant decrease in growth rate. Lyons and Kennedy (1981) found considerable evidence indicating that fishery handling techniques in the Florida *P. argus* fishery had a heavy impact on the stocks of sublegal lobsters, delaying or prohibiting their entry into the legal fishery.

Meyer-Rochow (1975) studied the eye of the western rock lobster, *P. cygnus*. Based on that work, Meyer-Rochow and Tiang (1981) concluded that exposure to bright light such as sunlight affects the rock lobster in several ways, all detrimental to survival, including an inability to see predators, even at moderately bright ambient light levels, inability to adjust to differing ambient light intensities, and difficulty in behaving according to a normal diurnal rhythm of activities. A study of fishery-related mortality in undersized and berried rock lobster, *P. cygnus*, showed that poor handling of lobsters before release caused high mortality (Anonymous, 1979, 1981; Brown and Caputi, 1983).

Gooding[1] reported on observations made on surface-released spiny lobsters and potential predators near Necker and Nihoa Islands in the NWHI. The objective of that preliminary study was to determine which fishes might be potential predators on surface-released lobsters. A number of previous casual observations of apparent predation on lobsters by jack crevally, *Caranx ignobilis*, or white ulua, as it is called in Hawaii, and galapagos shark, *Carcharhinus galapagensis*, had been reported by fishermen and scientists on fishing and research vessels. Thus, those two species were of particular interest. Tests were conducted in the presence of blue crevally, *Caranx melampygus*, single white ulua (no schools were seen), galapagos shark, reef whitetip shark, *Triaenodon obesus*, and gray reef shark, *Carcharhinus amblyrhynchos*. With the exception of a galapagos shark, which was observed to briefly mouth a lobster in midwater before releasing it, none of the fishes seen during those preliminary observations showed any inclination to prey on lobsters.

Sudekum[2] found that 1.5 percent of the white ulua he examined had *P. marginatus* and 1.5 percent had *P. penicillatus* remains in their guts. No lobster remains were in the *Caranx melampygus* he examined. Okamoto and Kawamoto (1980) also reported lobster remains in white ulua guts and, while conducting surveys at Pearl and Hermes Reef, they observed white ulua preying on *P. marginatus* which had fled from shelter when disturbed by divers[3]. De Crosta et al. (1984) found that guts of 65 *Carcharhinus galapagensis* he examined did not contain any lobster remains; however, 2 percent of *C. amblyrhynchos* and 11.1 percent of tiger shark, *Galeocerdo cuvier*, had *P. marginatus* remains in the gut contents.

The grouper, *Epinephelus quernus*, which is abundant in the NWHI, was considered a possible predator on released lobsters. However, although *E. quernus* are numerous in waters as shallow as 5 m at Kure Atoll and Midway (Hobson, 1980), they have not been reported in shallow waters in the southeastern part of the NWHI where the principal lobster grounds are located. In Hawaii, they are caught at bank drop-offs in depths >80 m. Seki (1984), in a study of the feeding habits of *E. quernus* caught with deep-sea handlines, did not find any lobster remains in the 67 specimens he examined. No *E. quernus* were seen during this study.

This report describes lobster release tests conducted during cruise 81-04 of the NOAA ship *Townsend Cromwell*. The cruise plan called for fishery survey operations throughout the NWHI which provided an opportunity to conduct tests incidentally when suitable conditions were encountered. Principal goals were to determine 1) under what conditions large schools of large white ulua prey on lobsters, 2) what other fishes are potential predators on released lobsters, 3) the probability of lobsters surviving predation when they are released at the surface and descend to the bottom in the presence of potential predators, particularly large white ulua, and 4) if lobsters contained in a bag from which they can be released at the bottom are less vulnerable to predation than when they are released at the surface and fall to the bottom.

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[1] Gooding, R. M. 1979. Observations on surface-released, sublegal spiny lobsters, and potential spiny lobster predators near Necker and Nihoa. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812, Admin. Rep. H-79-16, 8 p.

[2] Sudekum, A. E. 1982. Notes on the biology and feeding habits of *Caranx ignobilis* and *Caranx melampygus* in the Northwestern Hawaiian Islands. Seventh Albert L. Tester Memorial Symposium, Univ. Hawaii, Honolulu, April 1982. Abstr.

[3] Henry Okamoto, Hawaii Division of Aquatic Resources, 1151 Punchbowl Street, Honolulu, HI 96813. Pers. commun., December 1981.

Table 1.—Predation observations.

Date 1981	Local time	Dive no.	Depth (m)	Potential predators in the area			Type of lobster release
				Ulua	Galapagos shark	Gray shark	
Maro Reef							
7/29	1230	1	32	30-50	3		Free at surface
7/29	1345	2	32	25-40	4-5		Bag in midwater
7/30	0930	3	32	30-40	5		Bag, 5 feet from bottom
7/31	1015	4	30	15-20			Bag, 6 feet from bottom
Midway							
8/3	1330	1	15	2			Hand released from midwater
8/4	1000	2	17	2			Hand released from midwater
8/4	1030	3	17	2			Hand released from midwater
8/5	1400	4	15	1		5	Hand released from midwater
8/6	1430	5	12	2			Hand released from midwater
Pearl and Hermes Reef							
8/8	0915	1	18	75-100	3-5		Free at surface
8/8	0925	1	18	75-100	3-5		Bag in midwater
8/8	0935	1	18	75-100	3-5		Bag on bottom
8/8	1015	2	18	75-100	Several		Bag in midwater
8/8	1025	2	18	75-100	Several		Bag on bottom
8/8	1055	3	18	75-100	Several		Bag in midwater
8/8	1110	3	18	75-100	several		Bag on bottom
8/9	0900	4	18	75-100	Several		Bag in midwater
8/9	0915	4	18	75-100	Several		Bag on bottom
8/9	0955	5	18	75-100	Several		Bag in midwater
8/9	1005	5	18	75-100	Several		Bag on bottom

Procedures

Tests were conducted at Maro Reef, Pearl and Hermes Reef, and Midway (Table 1). The lobsters used in most of the tests had been trapped at either Necker Island, Gardner Pinnacles, or Maro Reef during lobster resource surveys which were concurrently being conducted. The trapped lobsters were held in the vessel's baitwell. Lobsters maintained under these conditions and fed cut fish remain in apparent good condition for several weeks. The animals were removed from the tank just before a test release. At Midway four tests were conducted with lobsters which had been hand captured in the immediate area shortly before testing. The smallest lobsters available were used. However, many of the animals, especially for the tests at Pearl and Hermes Reef, were considerably larger than the minimum legal retainable size. Three scuba-equipped observers carried a 16 mm movie camera and a 35 mm still camera.

At Maro Reef and Pearl and Hermes Reef, diving operations were conducted from the *Townsend Cromwell* while the ship was anchored. A standby diver-observer in an inflatable boat maintained position over the underwater observers. A system of hand signals was used by the divers to communicate with the surface observer who monitored the underwater operation through a lookbox or dive mask and relayed instructions to personnel on the vessel to lower the bag or release lobsters. The release bag consisted of a 1.85 × 1.85 m piece of loosely woven plastic mesh material with a grommet in the center. The line to lower the bag was tied to the grommet. The lobsters were placed on the material, and the four corners drawn up forming a bag and tied together with a slipknot using the line leading from the grommet which passed inside of the bag. A 2.3 kg lead weight was attached to the grommet and hung outside and below the bag. When the suspending line was jerked by a diver from a position 5-6 m above the bag (Fig. 2), it opened and released the lobsters. The combination of plastic mesh material, which did not trap air, and the weight permitted the bag to be lowered quickly. For some tests, the lobsters were dropped in batches from the deck of the vessel, similar to the manner in which they would be released from commercial fishing vessels. However, when animals were released in this way, they usually became so widely scattered as they descended, that it was difficult or impossible to observe and photograph subsequent events. If the bag was hung about half way to the bottom and opened by a diver from a position 5-6 m above it, the lobsters were not as widely dispersed, thus permitting far better control of the tests, and more opportunities to observe and photograph predator-prey interactions. Bottom releases using the bag were not actually on the bottom because the process of jerking the line to open the bag invariably resulted in the lobsters being released about 1 m above the bottom. A bag load consisted of 10-15 lobsters.

At Midway, tests were conducted from a small boat. Lobsters were carried in a net bag by one of the diver-observers and single animals were released in midwater while the two other divers observed.

Results

Maro Reef

The tests were conducted on the western side of Maro Reef in an area characterized by numerous 5-11 m pinnacles rising from depths of 30-34 m. The ship was anchored between the shallower areas in about 30 m. On the evening before the first predation tests, a 37 kg white ulua was caught by trolling in a school of large ulua in this area. It had a spiny lobster (8.6 cm CL) in its stomach.

Dive 1

The cage was suspended about 6 m

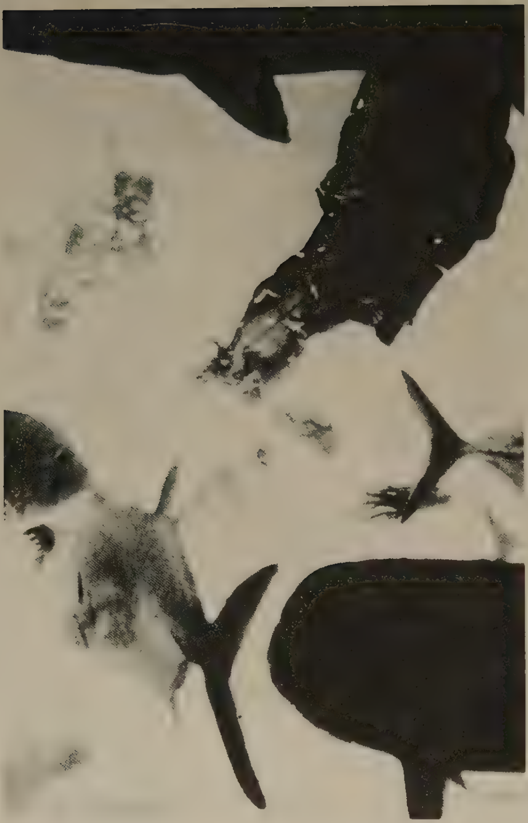

Figure 2.—Lobsters being released close to the bottom.

below the surface, and the diver-observers maintained about the same depth. There were 30-50 ulua estimated at 14-36 kg milling about in the immediate vicinity of the divers, and three 1.2-2 m galapagos sharks were circling well outside. On this dive, as on all subsequent dives during the cruise, the ulua did not show any signs of fear of the divers. Frequently they would swim within a few inches of an observer, or even touch him as they passed. Such was not the behavior of galapagos sharks, particularly the smaller ones, which usually stayed well away from human activity. Most of the lobsters released during the experiments at Maro Reef were <7.8 cm CL. Three lots of five lobsters each were released at the surface. As on previous experiments (Gooding, footnote 1), the lobsters did not swim (tail-flip) toward the bottom as is characteristic of spiny lobsters, but descended limply with tail slightly curled and legs spread. The ulua milled about among the sinking lobsters, and followed them to the bottom. Of the 15 lobsters released, we saw only 1 eaten by a fish. The lobster was taken in midwater and eaten tail first. Because of the wide scatter of the falling lobsters and reduced visibility due to turbid water during the dive, we were not able to make satisfactory observations in midwater nor were we able to see what became of the lobsters when they reached bottom.

Dive 2

Observations were made from the bottom. Water clarity had improved and because of the reflection from the sandy substrate, light conditions were better than in midwater. The bag containing 15 lobsters was opened about 5 m from the bottom. About 30 large uluas surrounded the bag as it was lowered from the ship. When the bag was opened, the fish immediately swam among the falling lobsters and nosed the lobsters as they were descending. No lobsters were eaten in midwater. About 8-10 lobsters landed in a group on the sandy bottom and quickly formed a close circular phalanx with their heads and antennae facing out, similar to the pod formations described by Kanciruk and Herrnkind (1978), but on a smaller scale. The remaining lobsters landed singly and assumed a more or less upright defensive posture, folded the tail beneath them, and moved the antennae in all directions (Fig. 3). The bottom was coral rubble or sand and afforded no shelter in the immediate vicinity. The lobsters did not attempt to leave the area. During the 10 minutes of bottom time which remained for the observers, the ulua showed relatively mild interest toward the lobsters. When a fish came close, the lobsters that landed singly would rear up and extend their antennae in the typical defense posture, always keeping their tails curled tightly in a protected position. Those forming a phalanx offered what appeared to be an effective defense, their vulnerable tails protected from attack. During the time available for observation, no lobsters were taken by the fish.

Dive 3

The next morning when about 30-40 large ulua were present, the bag containing fifteen <7.8 cm CL lobsters was opened about 1.5 m from the bottom. The fish showed strong interest in the bag as it was lowered, and when the lobsters were released, the fish immediately swam among them. When the lobsters reached the bottom, groups of two to three lobsters formed several small defensive groups and several single animals took on the characteristic defensive posture and behavior. The fish showed much more interest in the lobsters than on the previous test. Individual lobsters and members of a group were frequently flicked around or nosed by the fish. Several times we took lobsters from the bottom and rereleased them by hand about 6 m from the bottom. Several ulua would immediately follow the falling lobsters; however, no lobsters in midwater were ingested by the fish. After about 15 minutes and just before the observers had to ascend, two lobsters on the bottom were eaten in rapid succession by two different fish. This was the first time we were able to clearly observe predation and the associated behavior. It became clear that the frequent nosing and flicking about of the lobsters were attempts by the fish to place the lobster in a position where it could either be grabbed sideways and afterwards mouthed into a tail-first position and swallowed, or initially taken tail first and swallowed whole (Fig. 4). After being swallowed, the lobsters' antennae remained protruding from the two fishes' mouths for some time.

Dive 4

The next morning, the ship was anchored in the same general area and 15 bagged lobsters were released 1.5 m from the bottom at a depth of 32 m near 15-20 medium-sized (14-18 kg) ulua. The lobsters, singly or in groups, displayed the characteristic defensive behavior. The ulua showed considerable interest in the lobsters. The flicking and nosing action was successful in breaking up two small groups of lobsters; however, during the time we were able to remain on the bottom, no lobsters were eaten or taken into a fish's mouth.

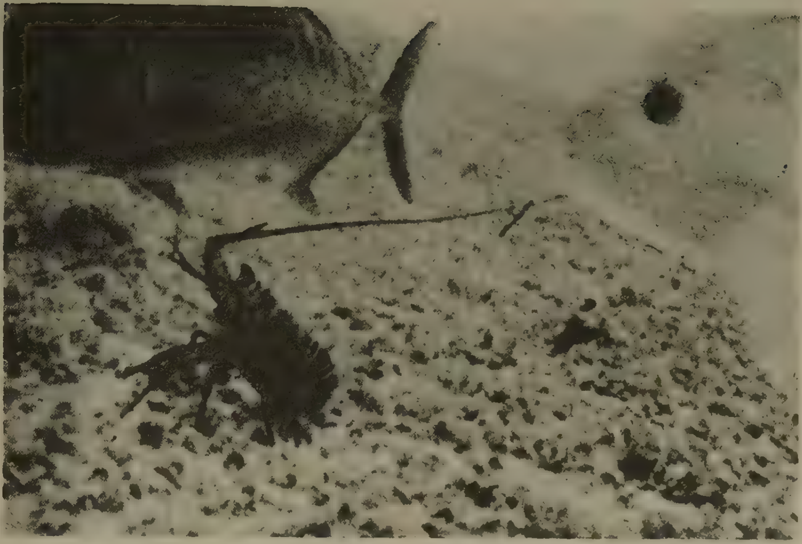

Figure 3.—Lobster in defensive posture.

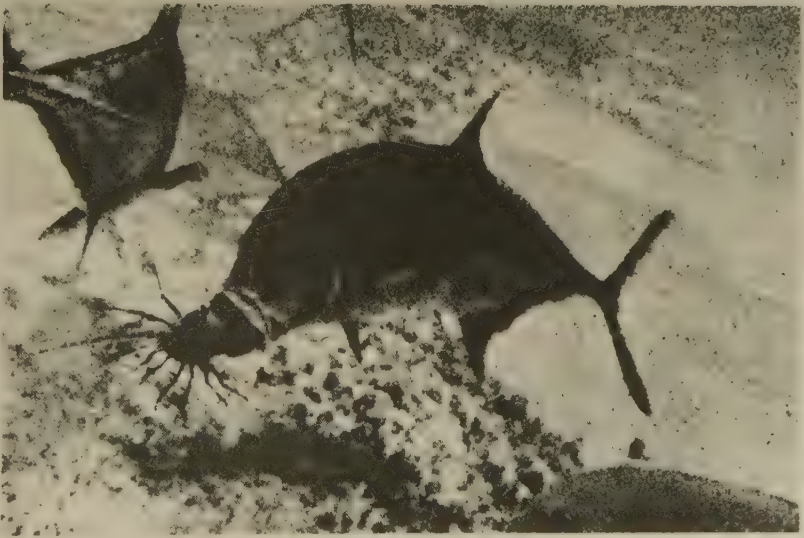

Figure 4.—An ulua swallowing a lobster tail first.

Midway

The tests were conducted from a small boat outside the barrier reef to the south of Sand Island in water 12-18 m deep. The procedure was for one diver-observer to hand-release a single lobster at a time in the presence of the potential predators. There were never more than two ulua present at once during the tests.

Dive 1

Two 18-28 kg ulua were in the area. The two lobsters which were released had been hand-caught a short time before in the same area. The first (about 8.0 cm CL) was released about 9 m from the bottom. It flipped its tail rapidly moving towards the bottom, pursued by both fish, and was caught sideways and swallowed tail first, just before it reached the bottom. Shortly afterward, a second lobster (about 6.0 cm CL) was released 6 m from the bottom. Just as it reached bottom, the same fish caught it and swallowed it tail first. The ulua continued to swim around in the area with two antennae protruding from its mouth until the observers surfaced.

Dive 2

Two 18-28 kg ulua started circling as soon as we entered the water. One observer carried two lobsters (7.5-8.0

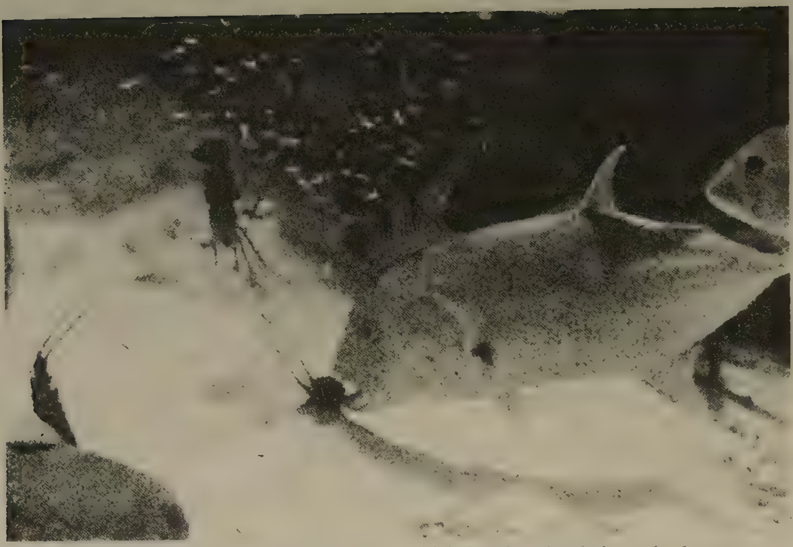

Figure 5.—An ulua attacking a lobster which has just landed on the bottom and has been unable to assume a defensive posture.

cm CL) which had been held in the *Townsend Cromwell's* baitwell. The first lobster was released about 8 m from the bottom. It started falling limply and was eaten tail first by one of the fish. When the other lobster was removed from the bag, the same ulua rapidly swam over, took the lobster from the diver's hand, and swallowed it.

Dive 3

In the same area as the previous dive and about 30 minutes later, the ulua that had taken the lobster from the diver's hand was still present. The antennae that had been protruding from its mouth were no longer visible. The other fish was not in sight. A lobster (about 8.5 cm CL), caught in the area a short time before, was released 8 m from the bottom and started a rapid tail-flip descent for the bottom. The fish took the lobster tail first and ate it. The swallowing process was noticeably slower with this lobster, the third eaten by the same fish within 45 minutes. When a fourth lobster of about the same size was released a few minutes later, the ulua, with the antennae of the previously eaten lobster still protruding from its mouth, followed the rapidly swimming lobster to the bottom, gave it a nudge, swam away, and showed no more interest. Apparently, three lobsters were all it could handle within that period.

Dive 4

A test was run the following day in the same general area 15 m deep where five gray reef sharks and one 18-23 kg ulua were present. A slightly undersized lobster which had been held in the ship's baitwell was released about 6 m above the bottom, then retrieved and re-released five times. The lobster elicited very little interest from the ulua or the sharks on any of these descents. The sharks left the area after a few minutes.

Dive 5

Shortly afterward, two ulua (of about 18 kg) were located in 12 m of water several hundred meters away. A 7-8 cm lobster which had been held in the *Cromwell*'s baitwell was released about 6 m from the bottom. Both fish attacked the lobster as it fell. One fish mouthed it several times, each time getting it sideways. The other fish, on a single pass, swallowed it tail first. During the following 15 minutes, more 7-8 cm CL lobsters were individually released in midwater about a dozen times. The same two ulua continued to show interest, following the lobsters to the bottom each time, but no more lobsters were eaten. Afterward, a speared wrasse, *Thalassoma* sp., about 20 cm long was released. Both fish pursued it and one ate it.

Pearl and Hermes Reef

The *Cromwell* was anchored in 19 m of water southwest of the small boat channel during the experiments. Conditions were excellent: The sea was calm, and water clarity was good.

Dive 1

An estimated 75-100 ulua, 11-45 kg, were present. The fish were bold and curious, and started milling around the divers as soon as they entered the water. There were also several galapagos sharks in the area, but they stayed well outside the center of activity, and usually were too far away to be visible.

Three tests were run during the dive. Ten lobsters each were released 1) from the ship at the surface, 2) from the bag in midwater about 8 m from the bottom, and 3) from the bag close to the bottom. On these tests and all subsequent tests, nearly all the lobsters released were >7.7 cm CL, ranging up to about 9.0 cm, the largest we had used thus far. The fish voraciously attacked and ate the lobsters as soon as they were released by all three of the release techniques. Of those animals that were released at the surface and in midwater, many were taken before they reached bottom. Those that reached bottom would immediately be surrounded by many fish trying to take a lobster. Occasionally, a fish would not be able to swallow a lobster and would spit it out, at which time many other fish would vie for it. There was often a clearly audible crunch when an animal was taken sideways. The ulua followed the bag down to the bottom, and many fish were immediately in among the lobsters as they were released. Most of the lobsters were taken before they could group into a defensive circle (Fig. 5). Those animals that survived the initial attack were immediately surrounded by a group of fish, and within a few seconds were eaten. None of the 30 lobsters survived for more than a few minutes after release.

Dives 2 and 3

Four more releases of 10 lobsters each in midwater and two near the bottom were made during two dives in the following 1.5 hours. The feeding activity of the school was undiminished throughout the tests and none of the released lobsters survived.

Dive 4

The tests were conducted in about the same area as on the previous day and probably with the same school of 75-100 ulua. There were also several galapagos sharks and gray sharks in the outlying area.

On the first test, when ten 8-9 cm CL lobsters were released from the bag about 10 m from the bottom, dozens of fish were around the bag as it opened. The lobsters were eaten so fast that it was difficult to see or film the action. All the lobsters were gone within 10 seconds and none reached the bottom. Shortly afterward another batch was released at the bottom. Again dozens of fish crowded around, and all 10 lobsters were gone within seconds of release. For the first time we saw a large ulua take a lobster head first into its mouth (Fig. 6). This fish swam around for several minutes with the tail protruding from its mouth, apparently unable to swallow it.

Dive 5

This was a repeat of the previous tests. Ten lobsters each were released 6 m from the bottom, and on the bottom. Most of those released in midwater were eaten before reaching bottom, but the four animals that reached bottom assumed the characteristic defensive posture and survived a little longer than on previous tests with this school of fish. Although many fish continuously circled each lobster, the last one was not eaten until several minutes later. On the following test, the last individual of a batch of 10 lobsters released on the bottom managed to survive for about 5 minutes, and our impression was that the rate of serious attempts by the ulua to capture lobster had decreased noticeably. On these last tests, it was evident that in this school only the larger fish were eating or mouthing the lobsters. It was, however, difficult to estimate accurately the size of the smallest fish which was able to ingest lobster of the size we were releasing, but our rough guess was about 16 kg.

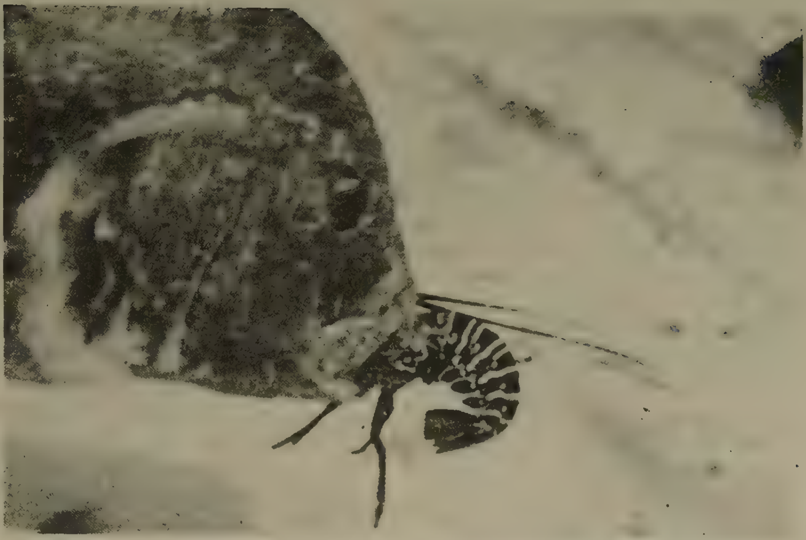

Figure 6.—A rare instance of an ulua attempting to swallow a lobster head first.

Sharks

During the tests at Maro Reef and Pearl and Hermes Reef, there usually were relatively small galapagos sharks (<2 m) in the vicinity. They always stayed well away and showed no inclination to approach released lobsters. While anchored off Necker Island one afternoon, we chummed with cut fish, and soon had several galapagos sharks ranging up to 2 m long around the vessel. While chumming continued, live lobsters tied to a light line were hung in the water among the chum. Sharks often came up to the lobsters with open mouth and turned just before reaching the lobster, or sometimes nosed it. The same thing was tried with lobster tails and heads, with the same results. However, in one test when the exoskeleton was removed from a tail and only the muscle was hung in the water, a shark took it immediately and swallowed it. The tests with a live lobster and complete tail were repeated while pouring fish blood into the water. The sharks went into a frenzy of feeding excitement, continuously nudging the lobster bait without taking them. Once the exoskeleton of a tail, from which the muscle had been removed, was taken into a shark's mouth for a moment and spat out. When fish (*Bodianus* sp.) were hung on a line, the shark bit them off and ate them without hesitation.

We did not have the opportunity to conduct experiments with *G. cuvier,* which are known lobster predators. Parrish et al. (1980) found that 11.1 percent of the tiger shark guts they examined contained remains of *P. marginatus.*

Discussion and Conclusions

Based on our experience, the presence of divers did not influence the feeding behavior of ulua toward spiny lobsters. However, galapagos sharks probably were affected. Usually galapagos sharks will swim very close to a vessel and show no hesitancy to approach anything resembling food that is tossed or hung in the water. During the diving observations in this study, galapagos sharks stayed well away. It seems probable that the behavior of the sharks during the tests was influenced by diver activity. Had no divers been present, the sharks might have come closer to the release bag or to the released lobsters. Thus the tests with diver-observers present may not have provided reliable data on whether galapagos sharks are potential predators on released lobsters. However, other evidence indicates that apparently this species is not a predator on spiny lobsters. De Crosta et al. (1984) did not find any lobster remains in the gut contents of the 65 galapagos sharks they examined, and our attempts to induce large galapagos sharks to ingest live lobsters or parts of lobsters, except peeled tail muscle, were unsuccessful.

Tests were conducted with large schools of large, white ulua at Maro Reef and at Pearl and Hermes Reef, and with pairs and individuals at Midway. There was considerable variation in the intensity of feeding by ulua on lobsters. The 14-45 kg fish at Pearl and Hermes Reef were voracious predators on lobsters, most of which were considerably larger than animals which would be released by commercial fishermen. At Maro Reef, large schools of ulua averaging 14-38 kg showed less interest when tested with smaller lobsters that should be more easily ingested. At Midway, pairs and single fish averaging about 25 kg, fed avidly on actively swimming lobsters up to about 8.5 cm CL.

In addition to state of satiation, a fish school's potential for lobster consumption presumably is related to fish size and size of school as well as lobster size. Other factors might include behavior of the lobsters and the behavioral elements that induce excitation of the fish.

The nature of the bottom over which lobsters are released could significantly influence the degree of predator success. However, the ability of animals to protect themselves on reaching bottom is not only contingent on availability of adequate shelter, but also on the lobsters' physical condition. Impairment to walking legs or antennae, or to an animal's physiological state would be detrimental to locomotion, or ability to adjust rapidly to the different environment.

Our observations were mostly made over bottoms which afforded little shelter. The test lobsters were apparently in good condition. However, except for those animals at Midway which were released shortly after capture, the test lobsters had been held in tanks for periods up to 2 weeks. The recently caught lobsters usually tail flipped to the bottom when released in midwater, whereas animals that had been held in captivity for some time always drifted limply to the bottom.

Brown and Caputi (1983) noted that *P. cygnus*, which had been exposed to air in direct sunlight for more than 30 minutes, drifted to the bottom with legs spread-eagle and tail either curled or extended on being returned to the water. Our test lobsters had not experienced such extreme exposure, but nevertheless, this markedly different behavior may indicate that lobsters which have experienced prolonged captivity are handicapped by an inability to adjust rapidly to a sudden reintroduction into their natural environment. Such animals may have a survival disadvantage compared with lobsters which are released shortly after capture. However, tests at Midway with recently caught lobsters that swam rapidly towards the bottom showed that they were also very vulnerable to ulua predation.

Clearly, white ulua are very effective predators on released lobsters. In the NWHI, a large school of feeding fish probably has the potential to consume a large percentage of the lobsters released freely at the surface from a commercial fishing vessel.

One way to safeguard most lobsters might be to release the animals from a bag near the bottom when there is reasonable assurance that white ulua are not in the vicinity and the substrate affords shelter. Since depths on the NWHI banks are too great to visually check the bottom type, such releases should be over known lobster fishing grounds. If the day's catch of lobsters below the legal minimum size were held in circulating tanks, handled with reasonable care, and a suitable time and place when ulua were not in the vicinity was chosen, this procedure should be effective. If followed, it is unlikely that predation from ulua during trap fishing would be detrimental to lobster populations on the NWHI grounds.

However, such a procedure may not be very practical. It is questionable that fishermen, after a long, hard day of hauling traps would be willing to devote the time and effort necessary to protect the released lobsters effectively. In addition, predation is probably not the principal hazard lobsters are exposed to when they are captured and released in the NWHI fishery. A recently completed study of fishery induced mortality in undersized rock lobster, *P. cygnus*, in the Western Australian fishery (Anonymous, 1979, 1981; Brown and Caputi, 1983) showed that there was a mortality of 15 percent of all undersized lobsters if they were transported more than 100 m away from their home reefs. The Australian work and that of Davis (1981) working with *P. argus*, showed that the more frequently lobsters were handled, the more damage they suffered, i.e., loss of appendages, exposure, etc. Physical damage increased mortality or decreased growth rate which prolongs the undersized period, and increases the toll of natural mortality in the population before the lobsters are recruited into the fishery at legal size. Brown[4] found that for average damage (1.5 appendages lost) and average exposure to the air (8 minutes) the mortality for undersized

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[4] Rhys S. Brown, Western Australian Marine Research Laboratories, Perth, Australia. Pers. commun., August 1982.

P. cygnus was approximately 15 percent. If these results can be extrapolated to the NWHI *P. marginatus* fishery, the inevitable handling which trapped and released lobsters undergo may eventually result in far greater mortality from displacement, physical damage, and exposure than the threat posed by white ulua predation.

The problem begins when undersized and berried animals are captured in the traps. In the Western Australia *P. cygnus* fishery, unobstructed escape gaps are required in all traps (Bowen, 1971). They found that with the currently required 5.4×30.5 cm escape gap, about 80% of all undersized lobsters (<7.6 cm CL) escape. Recent research indicates that if the gap widths were increased to 5.5 cm, escapement would increase. Their data show that with escape gaps the catch of legal-sized lobsters is not reduced (footnote 4).

A recent study with *P. marginatus* (Paul, 1984) essentially corroborates the Australian experience on the efficacy of escape gaps. Working with three types of gaps (all 6 cm wide), Paul found the overall average escapement of lobsters <8.1 cm CL was about 60 percent.

In the NWHI lobster fishery, if the numbers of undersized lobsters landed on fishing vessels were significantly reduced by requiring that traps be provided with escape gaps of specified dimensions, the potential mortality from exposure and handling as well as predation might be so reduced that no measures to directly protect lobsters from predation would be needed.

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Literature Cited

Anonymous. 1979. The fate of undersized rock lobsters returned to the sea. Fish. Ind. News Serv. 12(3):10-12.

________. 1981. Handling techniques costing W. A. rock lobster fishermen about $3.2 million a year. Fish. Ind. News Serv. 14(2):3-5.

Bowen, B. K. 1971. Management of the western rock lobster (*Panulirus longpipes cygnus* George). Proc. Indo-Pac. Fish. Counc. 14(Sect. 2):139-153.

Brown, R. S., and N. Caputi. 1983. Factors affecting the recapture of undersize western rock lobster *Panulirus cygnus* George returned by fishermen to the sea. Fish. Res. 2:103-128.

Davis, G. E. 1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull., U.S. 78:979-984.

De Crosta, M. H., L. R. Taylor, Jr., and J. D. Parrish. 1984. Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. *In* R. W. Grigg and K. Y. Tanoue (editors), Proc. Second Symp. Resour. Invest. Northw. Hawaiian Islands, Vol. 2, May 25-27, 1983, p. 75-95. Univ. Hawaii, Honolulu, UNIHI-SEAGRANT-MR-84-01.

Hobson, E. S. 1980. The structure of reef fish communities in the Hawaiian Archipelago: Interim status report. *In* R. W. Grigg and R. T. Pfund (editors), Proc. Symp. Status Resour. Invest. Northw. Hawaiian Islands, April 24-25, 1980, p. 57-70. Univ. Hawaii, Honolulu, UNIHI-SEAGRANT-MR-80-04.

Kanciruk, P., and W. Herrnkind. 1978. Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): Behavior and environmental correlates. Bull. Mar. Sci. 28:601-623.

Lyons, W. G., and F. S. Kennedy, Jr. 1981. Effects of harvest techniques on sublegal spiny lobsters and on subsequent fishery yield. Proc. Gulf Caribb. Fish. Inst. 33:290-300.

Meyer-Rochow, V. B. 1975. Larval and adult eye of the western rock lobster (*Panulirus longipes*). Cell. Tissue Res. 162:439-457.

________, and K. M. Tiang. 1981. Seeing lobsters are correctly treated. Catch '81, April: 17-21. New Zealand.

Okamoto, H., and P. Kawamoto. 1980. Progress report on the nearshore fishery resource assessment of the Northwestern Hawaiian Islands: 1977 to 1979. *In* R. W. Grigg and R. T. Pfund (editors), Proc. Symp. Status Resour. Invest. Northw. Hawaiian Islands, April 24-25, 1980, p. 121-130. Univ. Hawaii, Honolulu, UNIHI-SEAGRANT-MR-80-04.

Parrish, J., L. Taylor, M. DeCrosta, S. Feldkamp, L. Sanderson, and C. Sorden. 1980. Trophic studies of shallow-water fish communities in the Northwestern Hawaiian Islands. *In* R. W. Grigg and R. T. Pfund (editors), Proc. Symp. Status Resour. Invest. Northw. Hawaiian Islands, April 24-25, 1980, p. 175-188. Univ. Hawaii, Honolulu, UNIHI-SEAGRANT-MR-80-04.

Paul, L. M. B. 1984. Investigations into escape vent effectiveness and ghost fishing in captive populations of the spiny lobster, *Panulirus marginatus*. *In* R. W. Grigg and K. Y. Tanoue (editors), Proc. Second Symp. Resour. Invest. Northw. Hawaiian Islands, Vol. 2, May 25-27, 1983, p. 283-295. Univ. Hawaii, Honolulu, UNIHI-SEAGRANT-MR-84-01.

Seki, M. P. 1984. The food and feeding habits of the grouper, *Epinephelus quernus* Seale 1901, in the Northwestern Hawaiian Islands. *In* R. W. Grigg and K. Y. Tanoue (editors), Proc. Second Symp. Resour. Invest. Northw. Hawaiian Islands, Vol. 2, May 25-27, 1983, p. 179-191. UNIHI-SEAGRANT-MR-84-01.

Uchida, R. N., J. H. Uchiyama, R. L. Humphreys, Jr., and D. T. Tagami. 1980. Biology, distribution, and estimates of apparent abundance of the spiny lobster, *Panulirus marginatus* (Quoy and Gaimard), in waters of the Northwestern Hawaiian Islands: Part I. Distribution in relation to depth and geographical areas and estimates of apparent abundance. *In* R. W. Grigg and R. T. Pfund (editors), Proc. Symp. Resour. Invest. Northw. Hawaiian Islands, April 24-25, 1980, p. 121-130. Univ. Hawaii, Honolulu, UNIHI-SEAGRANT-MR-80-04.

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SEASONAL CYCLES OF FAT AND GONAD VOLUME IN FIVE SPECIES OF NORTHERN CALIFORNIA ROCKFISH (SCORPAENIDAE: *SEBASTES*)

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ABSTRACT

Seasonal changes in visceral fat volume and gonad volume are compared in five species of rockfish from northern and central California: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. In these species, visceral fat was deposited between spring and fall, at the same time as gametogenesis. Visceral fat declined in volume between fall and spring, coinciding with the decline in volume of testes and preceding the release of embryos in females. We suggest that increased feeding during the summer upwelling season provides the energy for simultaneous fat accumulation, gametogenesis, and perhaps somatic growth. During subsequent seasons of presumed food storage, these rockfishes may utilize visceral fat reserves for maintenance. This pattern of fat deposition and utilization may contribute to the long life and repeated reproduction of rockfishes, at the expense of current fecundity and growth.

Our data also suggest that rockfishes which spawn only once during the reproductive season have fat cycles of greater magnitude than those spawning more than once a year. Of the species that we studied, the apparent single spawners *S. entomelas* and *S. flavidus* have more northerly geographic distributions and larger fat cycles than the multiple spawners *S. goodei* and *S. paucispinis*. It is possible that the shorter and more pronounced productive season in the north leads to a greater need for fat reserves during winter and makes the wintertime production of additional batches of eggs energetically difficult.

The seasonal storage and utilization of lipid (and nonlipid) reserves are important in the metabolic activities and overall life histories of many animals (Love 1970; Shul'man 1974; Derickson 1976a and associated papers). While cycles of lipid storage and utilization are generally associated with seasonal changes in food availability (Derickson 1976b) or metabolic demands (Lawrence 1976), the functions of lipid storage are varied.

In many fishes, reserves are used primarily in reproduction, as indicated by complementary cycles of lipid content and reproductive activity (Lasker 1970; Shchepkin 1971a, b; Schevchenko 1972; Shul'man 1974; Tyler and Dunn 1976; Wootton and Evans 1976; Lasker and Smith 1977; Diana and MacKay 1979; Delahunty and de Vlaming 1980; Patzner 1980; Hunter and Leong 1981). The seasonal accumulation of sufficient reserves may be a prerequisite for sexual maturity in some fishes (Iles 1974), and the amount of material stored may influence fecundity (Tyler and Dunn 1976). Reserves may also be used in migration (Robertson and Wexler 1960; Dotson 1978; Glebe and Leggett 1981 a, b), and, when used in spawning migrations, may contribute indirectly to reproduction.

Slobodkin (1962) and Calow (1977), however, noted that fat deposition may actually detract from reproduction, particularly when fat deposition and reproduction are concurrent. In such cases, reserves are often used instead for maintenance during periods of food scarcity (Calow and Jennings 1977), enhancing the opportunity to reproduce in the future. Some fishes seem to use reserves both for reproduction and maintenance, when spawning occurs during periods of food scarcity or fasting (Wilkins 1967; MacKinnon 1972; Iles 1974; Newsome and Leduc 1975; Foltz and Norden 1977; Dawson and Grimm 1980; Pierce et al. 1980; Glebe and Leggett 1981 a, b). The interpretation of such cases is complex, since reproduction and maintenance may be competing concurrently for reserves.

Roberts (1979) noted that fat was deposited seasonally around the viscera of two species of shallow-water rockfish, *Sebastes mystinus* and *S. melanops*. He suggested that the cycle of fat deposition and utilization was related to seasonal changes in the abundance of food and to reproduction.

In this paper we examine the seasonal relationship

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between visceral fat volume and gonad volume in five offshore species of rockfish: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. Based on Roberts' suggestion and the general literature on fat cycles in fishes, we expected to find complementary cycles of fat and gonad volume, indicating that reserves are used in reproduction. We used visceral fat volume as a convenient index of the timing and magnitude of seasonal changes in reserves, explicitly assuming that reserves stored elsewhere would change coincidentally (Delahunty and de Vlaming 1980). Since we did not measure total reserves, our data on visceral fat volume cannot be applied to quantitative studies of energy budgets, but are most useful for examining seasonal changes and making comparisons within a group of closely related species.

The use of gonadal volume as an index of reproductive activity requires some explanation. In males, gonadal volume is a good index of the timing of gametogenesis. In females of this live-bearing genus, however, gametogenesis is often reflected only in the initial increase of gonadal volume. Following fertilization (which may occur some time after copulation, due to sperm storage [Sorokin 1961; Echeverria 1981[4]; Boehlert and Yoklavich 1984]), ovarian volume continues to increase during a gestation period that lasts a month or so (Moser 1967). There may be some postzygotic nutrition of embryos during this time (Boehlert and Yoklavich 1984), but much of the increase in volume is due to the accumulation of water (Moser 1967). In some species of *Sebastes* that spawn more than once a year, gametogenesis takes place again late in the reproductive season of females. Among the species considered here, *S. paucispinis* and *S. goodei* are clearly multiple spawners (Moser 1967; MacGregor 1970), and Echeverria[5] has presented some evidence for multiple spawning in *S. pinniger*.

MATERIALS AND METHODS

Party boat and commercial rockfish catches were sampled weekly, as a part of a large-scale study, by personnel from the National Marine Fisheries Service (Tiburon Laboratory) and the California Department of Fish and Game, at northern California fishing ports between Crescent City (lat. 41°N) and Morro Bay (35°N). The species sampled depended on the day's catch. Samplers measured the total length of each specimen to the nearest millimeter and removed the viscera and gonads for preservation in 10% Formalin[6] in seawater.

In the laboratory, fat tissue was dissected from the viscera and its volume estimated by water displacement in graduated cylinders. In some samples, a small amount of fat had liquified. The volume of this liquid was estimated and added to total fat volume. Gonads were also removed and their volume measured as above. The state of development of ovaries and testes was scored according to indices based mainly on gonad morphology and coloration (Moser 1967; Gunderson et al. 1980). Histological preparations of small gonads were used to confirm sex and state of maturity. Data for species, sex, total length, stage of maturity, and fat and gonad volume were stored using a computer.

Data on visceral fat volume were analyzed for collections made between March 1980 and February 1981, inclusive. Measurements of gonad volume were begun in June 1980 and continued until May 1981 to obtain a full year of data. For each species, data were pooled over all ports of collection and divided quarterly, as follows: spring (March-May), summer (June-August), fall (September-November), and winter (December-February). Quarterly division of data gave good sample sizes for most seasons, yet still allowed seasonal separation. Primary production is relatively low off California during fall and winter, but is greater during most of spring and summer, when coastal upwelling occurs (Bolin and Abbott 1963).

To facilitate comparisons, visceral fat volume and gonad volume were expressed as log-transformed power-function regressions of volume on fish length. The power equation is:

$$V = aL^b,$$

where V is volume, L is total length, and a and b are estimated parameters. This equation is often used to express the relationship between volumetric measures, such as fecundity, and linear measures, such as length (Bagenal 1978; Glebe and Leggett 1981a; de Vlaming et al. 1982). Logarithmic transformation to

$$\ln V = \ln a + b \ln L$$

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[4] Echeverria, T. 1981. Maturity in six species of rockfish (Pisces, Scorpaenidae, *Sebastes*). [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

[5] Echeverria, T. 1983. Maturity and seasonality of the rockfishes (Scorpaenidae: *Sebastes*) of central California. Unpubl. manuscr., 60 p. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

allows the use of standard least-squares regression techniques, and stabilizes variances (Bagenal 1978). Thus, rather than using ratios of fat or gonad volume to fish weight or length, which can be biased by allometric relationships between the measurements (Bagenal 1978; de Vlaming et al. 1982), we employed empirically derived regression lines. The use of power equations also allowed us to test hypotheses with standard statistical procedures. Regressions were calculated for each sex during each season. Although most of the analyses were for adults, seasonal regressions of visceral fat volume were also computed for juveniles when samples were large.

Differences between regressions of fat or gonad volume were tested by analysis of covariance, using the ratio:

$$F = \frac{(N - 4)\,(\mathrm{SS}_{\mathrm{com.}} - \mathrm{SS}_1 - \mathrm{SS}_2)}{2\,(\mathrm{SS}_1 + \mathrm{SS}_2)}$$

where SS_1 and SS_2 are the residual sums of squares about the separate regressions, $\mathrm{SS}_{\mathrm{com.}}$ is the residual sum of squares for a common regression, and N is the number of specimens (Kleinbaum and Kupper 1978). When regressions differed significantly, the direction of differences was assessed by examining the positions of the regression lines and of calculated volumes at mean fish length. We chose to display only the calculated volumes at mean length, to simplify the presentation of data. The mean of ln (total length) was determined for all specimens of a sex and species included in the annual analysis. For each season and sex, the estimated value of ln (volume) at the mean of ln (length) (designated $\hat{Y}$) was calculated from the appropriate regression. We intend these point values to be used only for making comparisons within our data. The regression lines themselves best represent fat or gonad volume, and we present the parameters for these regressions. See Guillemot (1982) for scatter diagrams of raw data and regression plots.

The estimated values of fat volume at mean length were also used in an index of the relative amplitude of fat cycles. This index was the antilog of the difference between estimated ln (fat volume) in peak and low seasons, and is equivalent to the ratio of peak season:low season fat volume.

We compared fat cycles of males and females within a species by qualitatively noting differences in the timing and amplitude of fat cycles, and by statistically comparing fat regressions during peak and low seasons of fat volume. The latter comparisons were carried out by analysis of covariance, as above.

In comparing fat cycles among species, we noted differences in the timing of fat cycles and differences in the amplitude of cycles. We also assessed differences in the absolute volume of fat stored by applying analyses of covariance to the peak-season fat regressions of the different species.

RESULTS

Seasonal Cycles of Fat and Gonad Volume in Adults

In most seasons, moderate to low correlations (0.5 and below) existed between ln (visceral fat volume) and ln (total length), indicating a fair amount of scatter about the regressions (Table 1). Lower correlations occurred mainly in seasons of low fat volume (cf. Fig. 1). The slopes of most regressions were not significantly different from 3.0 (Table 1), indicating a proportionate relationship between fat volume and fish length. Slopes significantly smaller than 3 occurred in seasons of low fat volume (winter and spring), and in general slopes from seasons of low fat volume were smaller than those from seasons of higher fat volume. During seasons of low fat volume, fish of all sizes tended to have little fat, accounting in part for some of the lower correlations. Some slopes were significantly greater than 3 during seasons of high fat content (*S. entomelas* females, *S. paucispinis* males, *S. pinniger* females, and *S. flavidus* females), indicating disproportionately greater fat content in larger fish. Correlations between ln (gonad volume) and ln (total length) were generally high (Table 2), and showed no marked relation with season (Fig. 2). Below, we first examine the fat and gonad cycles for adults of each species separately, and then briefly compare the cycles of different species.

Sebastes entomelas

Visceral fat content changed significantly during the year in both male and female *S. entomelas* (Fig. 1). In females, where all seasonal regressions of ln (visceral fat volume) on ln (total length) differed significantly from each other, fat content increased from a low in spring to a peak in fall, and then declined in winter (Fig. 1). In males, neither the spring and winter nor the summer and fall fat regressions differed significantly (Fig. 1). Visceral fat volume in males increased after spring to a peak spread through summer and fall, and then declined in winter (Fig. 1). During the fall, when both sexes had large volumes of visceral fat, fat content of males barely

TABLE 1.—Seasonal regressions of ln (visceral fat volume, ml) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California. Slopes significantly different from 3 are indicated (? = $P < 0.1$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Species and season	Females				Males			
	Sample size	Intercept	Slope	*r*	Sample size	Intercept	Slope	*r*
S. entomelas								
Spring	118	–21.752	3.845	0.240	88	–12.267	2.341	0.138
Summer	102	–23.875	4.335*	0.578	58	–32.427	5.795?	0.456
Fall	81	–28.715	5.184**	0.581	57	–20.654	3.908	0.459
Winter	163	–18.442	3.400	0.428	84	–19.524	3.538	0.251
S. paucispinis								
Spring	117	–10.334	1.988?	0.314	115	–17.544	3.150	0.443
Summer	116	–16.415	2.982	0.576	127	–16.120	2.978	0.553
Fall	75	–12.957	2.500	0.462	101	–24.053	4.259**	0.693
Winter	82	–1.269	0.633***	0.165	83	–9.847	1.942*	0.389
S. goodei								
Spring	193	–12.741	2.220	0.272	51	–14.555	2.671	0.281
Summer	219	–10.780	2.027	0.221	80	–11.827	2.299	0.403
Fall	140	–14.895	2.763	0.499	68	–17.686	3.228	0.334
Winter	183	0.253	0.155***	0.020	55	0.783	–0.026?	–0.002
S. pinniger								
Spring	23	–16.134	2.980	0.400	38	–16.581	3.006	0.445
Summer	61	–28.391	4.957***	0.786	103	–17.213	3.152	0.455
Fall	32	–24.771	4.453	0.579	37	–14.859	2.825	0.593
Winter	18	–24.371	4.289	0.529	14	–28.849	5.063	0.538
S. flavidus								
Spring	73	8.221	–1.038**	–0.099	71	–18.255	3.298	0.259
Summer	143	–24.044	4.323**	0.605	88	–10.960	2.152	0.240
Fall	147	–14.050	2.771	0.468	112	–8.652	1.777	0.212
Winter	69	–2.946	0.743*	0.092	72	–14.442	2.575	0.227

exceeded that of females. Fat regressions at the low point in spring did not differ significantly (Table 3).

As expected, gonad volume changed significantly during the year in both sexes of *S. entomelas* (Fig. 2). In males, the volume of testes increased dramatically from a low in spring to a peak in summer, and then declined through fall and winter (Fig. 2). In females, the volume of ovaries increased very slightly between spring and summer, and then increased greatly in fall and winter (Fig. 2).

Sebastes paucispinis

Visceral fat volume changed significantly during the year in males and females of *S. paucispinis* (Fig. 1). In females, fat content did not change significantly between spring and summer, but increased from summer to a peak in fall, to decline slightly in winter (Fig. 1). In males, visceral fat accumulated between spring and summer, remained about constant from summer to fall, and declined in winter (Fig. 1). During the nominal peak season in fall, fat content of females was significantly greater than that of males, while the regressions for fat content during the nominal low points in spring did not differ significantly (Table 3).

Ovarian volume in *S. paucispinis* reached its low point during summer, increased with vitellogenesis in fall, increased again with embryogenesis and/or further vitellogenesis in winter, and then declined in spring (Fig. 2). The volume of testes increased from spring into summer, continued to increase slightly in fall, and declined in winter (Fig. 2).

Sebastes goodei

Visceral fat volume in female *S. goodei* increased from spring through summer to a peak in fall, and declined in winter (Fig. 1). In male *S. goodei*, visceral fat volume increased from low levels in spring to a peak in summer, declined slightly in fall, and decreased again in winter (Fig. 1). The fat content of females during their fall peak exceeded that of males during their summer peak, while there was no significant difference in fat content during the low seasons of spring for females and winter for males (Table 3).

Ovarian volume increased slightly between spring and summer in females of *S. goodei*, and then grew more rapidly through fall and winter (Fig. 2). The volume of testes increased greatly between spring and summer in males of *S. goodei*, and then declined through fall and winter (Fig. 2).

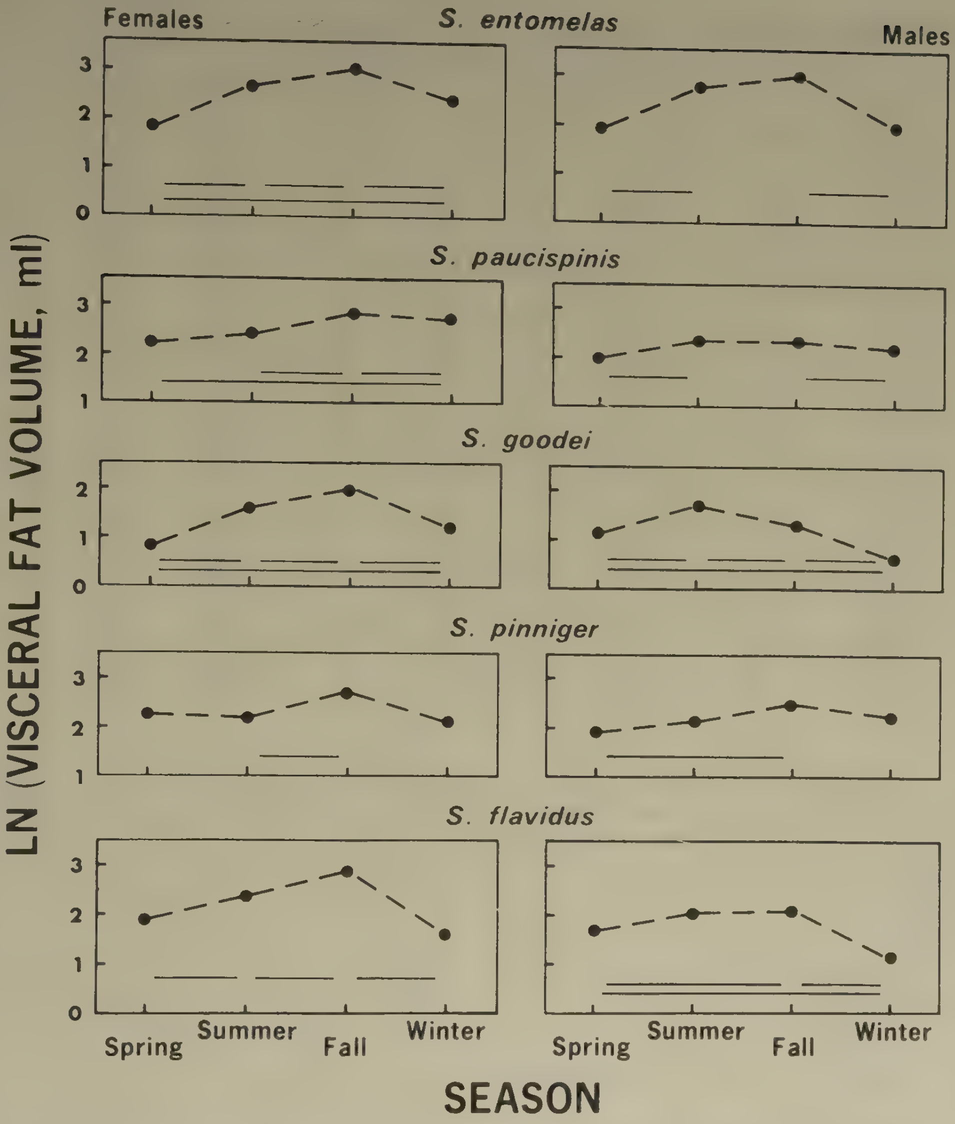

FIGURE 1.—Seasonal variation of visceral fat volume in adults of five species of *Sebastes* from northern and central California. For each species and sex, points are estimates of ln (fat volume) at the overall average of ln (total length) for specimens of that species and sex examined during the year. Estimates were derived from the seasonal regressions of ln (visceral fat volume) on ln (total length) (Table 1). A horizontal line between two seasons means that the fat regressions for those two seasons differed significantly ($P \leqslant 0.05$) by analysis of covariance. The upper of the two rows of horizontal lines are for adjacent seasons in the graph. The lower horizontal line is for winter and spring. The absence of a horizontal line means that the regressions did not differ significantly. Annual averages of ln (total length, mm) are *S. entomelas* females, 6.13, and males, 6.08; *S. paucispinis* females, 6.31, and males, 6.20; *S. goodei* females, 6.11, and males, 5.88; *S. pinniger* females, 6.11, and males, 6.14; and *S. flavidus* females, 6.11, and males, 6.04. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

TABLE 2.—Seasonal regressions of ln (gonad volume, mL) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California.

Species and season	Females				Males			
	Sample size	Intercept	Slope	*r*	Sample size	Intercept	Slope	*r*
S. entomelas								
Spring	217	−36.259	6.226	0.787	93	−40.725	6.738	0.709
Summer	17	−50.148	8.148	0.908	18	−42.341	7.386	0.644
Fall	65	−58.734	10.187	0.781	33	−10.442	1.930	0.191
Winter	177	−40.049	7.249	0.532	115	−18.856	3.207	0.403
S. paucispinis								
Spring	113	−26.341	4.541	0.640	163	−36.055	5.933	0.855
Summer	78	−34.265	5.767	0.919	105	−36.360	6.130	0.807
Fall	78	−37.533	6.386	0.833	118	−28.802	4.935	0.845
Winter	118	−34.058	5.946	0.647	127	−17.757	3.014	0.508
S. goodei								
Spring	146	−34.372	5.961	0.785	60	−20.612	3.552	0.332
Summer	166	−32.127	5.617	0.798	63	−12.733	2.386	0.283
Fall	176	−17.064	3.293	0.460	93	−29.433	5.095	0.772
Winter	184	−27.812	5.151	0.495	71	−17.172	2.886	0.214
S. pinniger								
Spring	21	−23.843	4.181	0.694	35	−49.963	8.230	0.799
Summer	22	−51.129	8.611	0.902	43	−60.352	10.175	0.939
Fall	31	−50.164	8.448	0.889	40	−45.336	7.564	0.845
Winter	21	−34.798	6.022	0.538	14	−65.227	10.657	0.904
S. flavidus								
Spring	100	−29.422	5.083	0.707	138	−31.837	5.228	0.499
Summer	83	−33.961	5.892	0.852	50	−54.152	9.204	0.759
Fall	162	−47.425	8.155	0.822	134	−38.906	6.649	0.690
Winter	53	−30.680	5.592	0.575	80	−23.743	3.927	0.555

TABLE 3.—Comparisons of fat volume between males and females during peak and low fat seasons in five species of *Sebastes*. If not defined statistically, peak and low seasons were selected on the basis of regression positions. $\hat{Y}$, the estimated ln (fat volume) at the overall average of ln (total length), is presented as an indication of regression position (Fig. 1). If male and female fat regressions differed significantly ($P \leq 0.05$) by analysis of covariance, their relative fat volumes are indicated. NS denotes regressions that did not differ significantly.

Species	Females		Males		Comparison
	Season	$\hat{Y}$	Season	$\hat{Y}$	
S. entomelas					
Peak	Fall	3.07	Fall	3.09	♂ > ♀
Low	Spring	1.82	Spring	1.96	NS
S. paucispinis					
Peak	Fall	2.81	Fall	2.35	♀ > ♂
Low	Spring	2.20	Spring	1.99	NS
S. goodei					
Peak	Fall	1.98	Summer	1.70	♀ > ♂
Low	Spring	0.82	Winter	0.63	NS
S. pinniger					
Peak	Fall	2.69	Fall	2.49	NS
S. flavidus					
Peak	Fall	2.87	Fall	2.08	♀ > ♂
Low	Winter	1.59	Winter	1.12	NS

Sebastes pinniger

Cycles of visceral fat volume were poorly defined in *S. pinniger*. In females, only the summer and fall fat regressions differed significantly, suggesting a peak in fat content during the fall (Fig. 1). In males, no two consecutive seasons differed significantly in fat content, and the only two seasons that differed significantly at all were spring and fall (Fig. 1). Thus, males may also have had peak fat content during fall, but their fat cycle was not pronounced. The visceral fat content of males and females did not differ significantly during their apparent fall peaks (Table 3).

The ovarian cycle of *S. pinniger* was also poorly defined in our data. Ovaries increased significantly in volume between spring and summer (Fig. 2). No other seasons differed significantly, but a peak in winter is indicated in Figure 2. In males, gonadal volume increased dramatically from spring to a peak in summer, remained fairly high in fall, and declined in winter (Fig. 2).

Sebastes flavidus

Visceral fat volume in female *S. flavidus* increased from spring through fall, and then declined in winter (Fig. 1). Male *S. flavidus* exhibited a gradual increase in fat content between spring and fall, followed by a decline to minimal fat levels in winter (Fig. 1). Fat content of females exceeded that of males during their fall peaks, and the difference in fat content during their winter lows was not significant (Table 3).

Ovarian volume in *S. flavidus* showed a pattern similar to most of the rest of the species: an increase

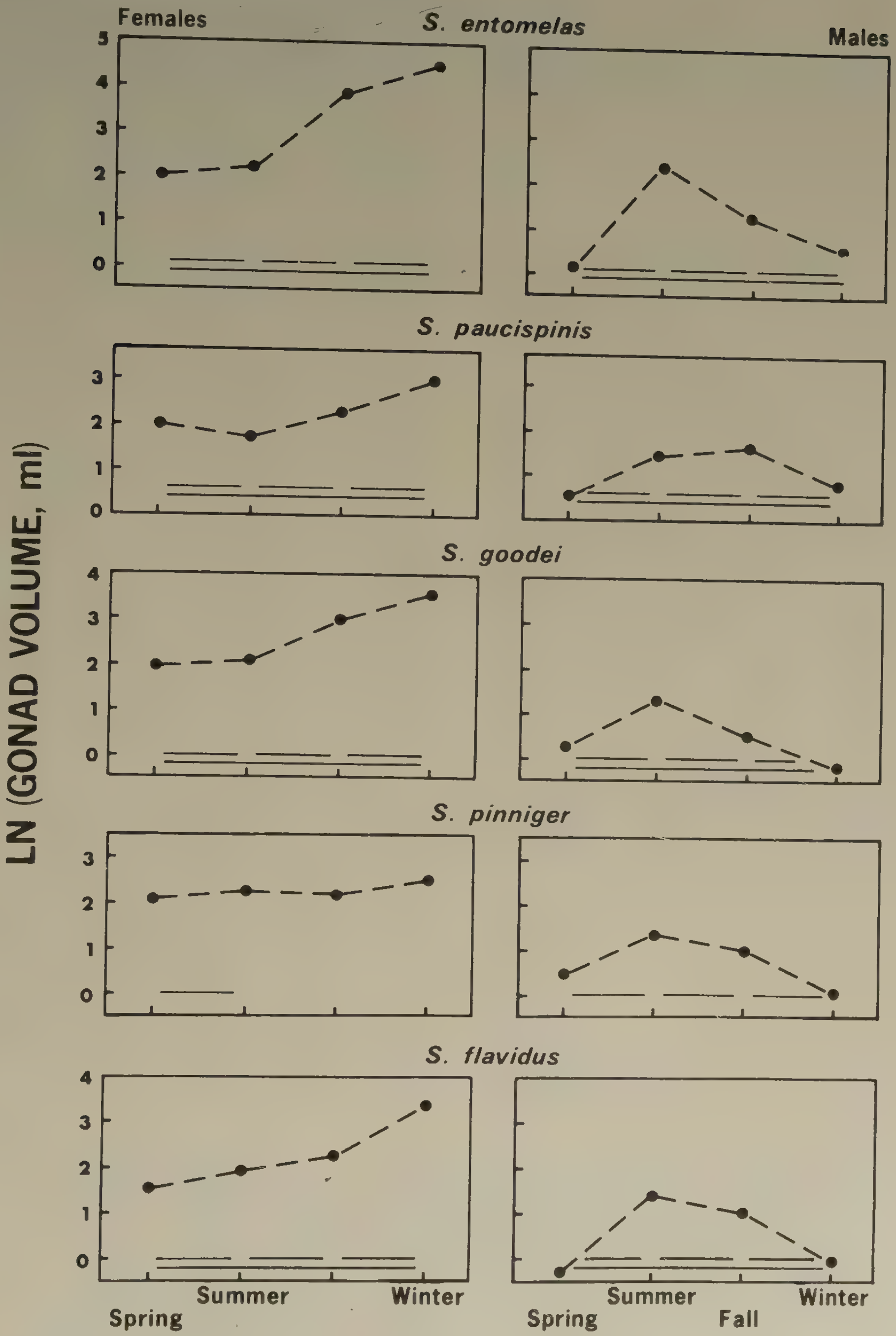

FIGURE 2.–Seasonal variation of gonad volume in adults of five species of *Sebastes* from northern and central California, as in Figure 1. Averages of ln (total length, mm) used in estimating gonadal volume are *S. entomelas* females, 6.14, and males, 6.06; *S. paucispinis* females, 6.24, and males, 6.17; *S. goodei* females, 6.09, and males, 5.88; *S. pinniger* females, 6.20, and males, 6.13; and *S. flavidus* females, 6.09, and males, 6.04. Seasons: spring (March-May 1981), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

from low volume in spring to peak volume in winter (Fig. 2). In males, the volume of testes increased from spring to a peak in summer, declined slightly in fall, and fell greatly in winter (Fig. 2).

Summary and Comparison of Adult Fat Cycles

In all species studied, visceral fat volume was high, if not at a peak, during fall. In males, fat content was usually high during summer as well. In male *S. entomelas*, *S. paucispinis*, and *S. flavidus*, summer and fall fat content did not differ significantly, and in male *S. goodei* the fat content in summer was actually greater than in fall. Summertime fat content was relatively high in female *S. entomelas*, *S. goodei*, and *S. flavidus*, but in females of all species the fat content increased to a peak in fall. Winter and spring were usually the seasons of low fat volume in both sexes. Little pattern existed in *S. pinniger*, except that fat volume appeared to reach a peak in fall.

Both the relative amplitude of fat cycles and peak fat volume differed among the species and sexes. In male and female *S. entomelas*, *S. goodei*, and *S. flavidus*, the fat volume of average-sized fish changed by about a factor of three during the year (Table 4). The amplitude of the fat cycle was lower in *S. paucispinis* and *S. pinniger*, where there was less than a twofold change in fat content between peak and low seasons (Table 4). Among females, *S. entomelas* and *S. flavidus* generally had higher peak fat volumes than the other species (Table 5). Among the other three species, peak fat content of females seemed to decrease from *S. pinniger* to *S. paucispinis* to *S. goodei* (Table 5). Females of *S. entomelas* and *S. flavidus*, then, possessed high-volume, high-amplitude fat cycles, while *S. pinniger* and *S. paucispinis* had low-volume, low-amplitude fat cycles, and *S. goodei* showed low volume and relatively high amplitude. The peak fat volume in male *S. entomelas* far exceeded that of the remaining species, most of which had relatively similar fat-length relationships during peak seasons (Table 5). Thus among males, only *S. entomelas* showed a high-volume, high-amplitude fat cycle. Males of *S. flavidus* and *S. goodei* possessed fat cycles of low volume and moderately high amplitude, and *S. paucispinis* and *S. pinniger* had cycles of low volume and low amplitude, like the females of these species.

TABLE 4.—Relative amplitude of fat cycles in five species of *Sebastes*. The ratio of estimated peak season: low season fat volume is presented for each species and sex, and is used as an index of cycle amplitude. Ratios are the antilogs of the differences between estimated ln (fat volume) at the average of ln (total length) in peak and low fat seasons (Fig. 1, Table 3).

	Amplitude	
Species	Females	Males
S. entomelas	3.50	3.10
S. paucispinis	1.83	1.44
S. goodei	3.20	2.91
S. pinniger	1.67	1.84
S. flavidus	3.61	2.64

Fat Cycles in Juveniles

Fat cycles were examined in juveniles of male and female *S. paucispinis*, and of female *S. pinniger* and *S. flavidus*, where seasonal sample sizes were large enough to permit analysis (Table 6). In *S. paucispinis*, juvenile females appeared to reach a peak in fat content during winter, but in juvenile males there were no significant differences among the seasonal regressions (Fig. 3). In *S. pinniger*, juvenile females

TABLE 5.—Comparisons of the peak-season regressions of ln (fat volume) on ln (total length) for different species of *Sebastes*. Comparisons were made by analysis of covariance. For significantly differing regressions ($P \leq 0.05$), the comparative fat volumes are indicated (based on the positions of the regressions, cf. Fig. 1, Table 1), unless intersecting lines made position difficult to interpret. NS denotes regressions that did not differ significantly.

	S. paucispinis	*S. goodei*	*S. pinniger*	*S. flavidus*
Females				
S. entomelas	S.e. > S.pa.	S.e. > S.g.	NS	NS
S. paucispinis		S.pa. > S.g.	NS	S.pa. < S.f.
S. goodei			S.g. < S.pi.	S.g. < S.f.
S. pinniger				S.pi. < S.f.
Males				
S. entomelas	S.e. > S.pa.	S.e. > S.g.	S.e. > S.pi.	S.e. > S.f.
S. paucispinis		intersection	S.pa. < S.pi.	intersection
S. goodei			NS	NS
S. pinniger				NS

possessed little fat in the spring, and higher levels in summer through winter (Fig. 3). Fat content in juveniles of female *S. flavidus* peaked in fall (Fig. 3).

TABLE 6.—Seasonal regressions of ln (visceral fat volume, mL) on ln (total length, mm) in juveniles of three species of *Sebastes* from northern and central California.

Species and sex	Season	Sample size	Intercept	Slope	*r*
S. paucispinis					
females	Spring	140	−19.637	3.510	0.325
	Summer	138	−26.793	4.669	0.455
	Fall	55	−23.626	4.189	0.419
	Winter	67	−29.508	5.205	0.719
males	Spring	92	−10.309	1.976	0.157
	Summer	86	−22.626	3.969	0.362
	Fall	10	−48.866	8.324	0.599
	Winter	21	−27.486	4.818	0.766
S. pinniger					
females	Spring	41	−21.012	3.655	0.402
	Summer	76	−21.794	3.859	0.624
	Fall	37	−36.539	6.383	0.875
	Winter	20	−18.568	3.345	0.651
S. flavidus					
females	Spring	21	−22.796	4.080	0.388
	Summer	70	−8.502	1.642	0.260
	Fall	53	−36.450	6.558	0.639
	Winter	19	−9.906	1.848	0.361

Thus, in three of the four groups analyzed, fat content of juveniles varied during the year. The timing of the apparent cycles was similar to that of adults. The amplitude of the fat cycle in juveniles of female *S. paucispinis* and *S. pinniger* (less than twofold change in fat volume) was similar to adult amplitude. In female *S. flavidus*, the amplitude of the fat cycle in juveniles (less than twofold change) was lower than in adults. As adults, *S. flavidus* showed high-amplitude fat cycles, while *S. paucispinis* and *S. pinniger* showed low-amplitude cycles.

DISCUSSION

Clear cycles of visceral fat volume and gonadal volume occurred in both sexes of *S. entomelas*, *S. paucispinis*, *S. goodei*, and *S. flavidus*. The fat cycles of male and female *S. pinniger* were less well-defined, as was the gonadal cycle of female *S. pinniger*. Many of the female *S. pinniger* we examined were relatively small adults. This may account, at least in part, for the small and ill-defined fat and gonad cycles, as the fat cycles of female *S. flavidus* increased in amplitude from juveniles to adults.

Visceral fat volume generally increased propor-

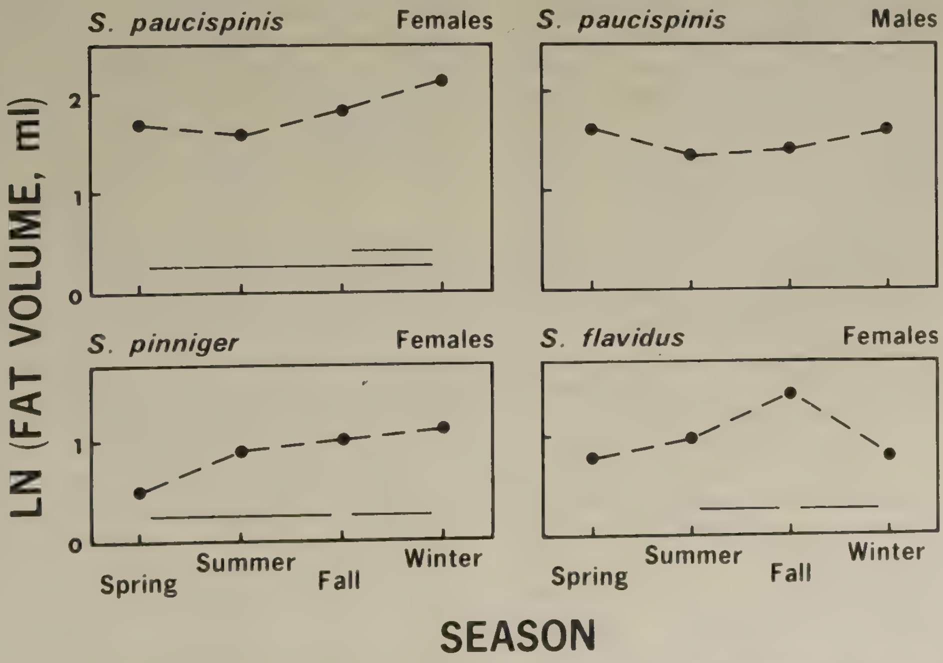

FIGURE 3.—Seasonal variation of visceral fat volume in the juveniles of five species of *Sebastes*, as in Figure 1. Averages of ln (total length, mm) used in estimating fat volume are *S. paucispinis* females, 6.08, and males, 6.04; *S. pinniger* females, 5.88; and *S. flavidus* females, 5.78. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

tionately with fish volume, since most slopes of ln (fat volume) on ln (length) were near 3. Slopes smaller than 3 occurred in those seasons when fish of all sizes had little fat. Some slopes during seasons of high fat volume were significantly greater than 3, indicating that larger fish had disproportionately greater fat volume than smaller fish. This was particularly true of, but not limited to, the species and sexes with high-magnitude fat cycles (males and females of *S. entomelas* and females of *S. flavidus*). It would be interesting to discover whether larger females of *S. pinniger* have high-amplitude fat cycles, since the slopes of the fat regressions for female *S. pinniger* were relatively high.

The dependence of fat volume on fish size and season of collection, while applicable on average, does not apply to every individual. The scatter about the regressions of fat volume on length was large. Some of the scatter was probably due to errors in measurement, but a large part was real. We have observed large differences in the amount of visceral fat among fish of the same size and sex in the same collection. The reasons for such variation may be difficult to resolve, since it is difficult to know the history of individuals collected in the field.

However, our data were adequate in most species to detect seasonal changes on average. We wanted to compare the timing of fat cycles and gonad cycles, and thus learn something of the function of fat storage in rockfish. Our initial hypothesis was that stored fat would be used in reproduction, based on Roberts' (1979) observations.

The data for males do not support this hypothesis. Fat and gonad cycles were nearly coincident, with peaks in both cycles occurring in fall and/or summer and lows in winter/spring. Thus the energy for gonadal growth was probably derived from current ingestion, not from material previously stored as fat. Maximum somatic growth also coincides with the summertime growth of testes and fat deposits (e.g., Love and Westphal 1981), so all three processes may be competing for energy consumed during this time.

The situation is more complicated in females. Some fat was deposited between spring and summer in females of *S. entomelas*, *S. goodei*, and *S. flavidus*, and females of all species gained fat between summer and fall. Some gonadal growth took place between spring and summer in females of all species except *S. paucispinis*. In all but *S. pinniger*, however, ovarian volume increased steadily between summer and winter. The growth of ovaries through fall was due largely to vitellogenesis, while the greater growth of ovaries into winter was due primarily to embryogenesis and hydration of ova (Moser 1967). Additional vitellogenesis probably occurred during winter in the multiple spawners, *S. paucispinis* and *S. goodei* (Moser 1967; MacGregor 1970).

In females, then, fat deposition usually began in summer, perhaps slightly before the initiation of vitellogenesis, but continued into the main period of vitellogenesis between summer and fall. Thus, like males, females of these species deposited fat more or less concurrently with gonadal maturation and somatic growth. The depletion of visceral fats occurred between fall and spring in females of most species, during and after gestation. It is possible that fat reserves are used for the maturation of additional ova in multiple spawners or are involved in the nutrition of embryos (Boehlert and Yoklavich 1984), but as in males, reserves are not used in the initial development of gonads.

There were two main differences in the fat cycles of males and females: females usually had larger fat cycles than males, and the peak fat volume of females occurred in fall, while fat volume in males usually reached a plateau that spread through summer and fall. It is possible that courtship activity in males (Helvey 1982) draws energy from fat deposition between summer and fall, or that this activity draws time from feeding. As a result, females may continue to fatten after fat deposition ceases in males. It is also possible that females require more reserves in winter and they somehow are able to acquire these extra reserves.

The synchronous depletion of reserves in males and females, however, indicates a common function for such reserves. We suggest two possible functions:

First, some rockfish may migrate during the period of fat depletion. Love (1981) presented evidence for seasonal movements in *Sebastes paucispinis* and *S. entomelas* off southern California, but had no data on the extent or direction of movement. Females of *S. alutus* undertake seasonal migrations covering as much as 300 m of depth (summarized in Gunderson 1977). Lenarz (pers. obs.) found evidence of seasonal movement in female *S. jordani*. Several species of rockfish undertake little or no seasonal migration, including *S. flavidus* from shallow waters off Alaska (Carlson and Barr 1977). Since seasonal migrations in rockfish may not be long and seem to occur primarily in females, we suggest that other possibilities be ruled out before accepting migration as a major use of fat reserves.

Second, we suggest that fat reserves are used for maintenance during wintertime periods of reduced food availability. Fattening, as well as growth and initial gametogenesis, occurs during and shortly after the spring-summer upwelling period, and depletion occurs during and after a time of lower primary production (Bolin and Abbott 1963). Roberts (1979) noted that several species of inshore rockfish near Monterey consumed more food during the summer, when macroplankton (euphausiids) and juvenile rockfish were abundant. During the nonupwelling season, juvenile rockfish and macroplankton were less abundant, and adult rockfish consumed less food. Love and Westphal (1981) found less food in the stomachs of *S. serranoides* during the nonupwelling season near Morro Bay. Gunderson (1977) noted a "summer feeding season" in *S. alutus*. Hobson and Chess[7], however, found the gelatinous prey of *S. mystinus* to be more abundant during nonupwelling periods off northern California. There is only limited information on the seasonal food habits of the five species studied here. *Sebastes paucispinis* is largely piscivorous (Phillips 1964), while *S. entomelas*, *S. goodei*, *S. pinniger*, and *S. flavidus* feed on macroplankton and small fish (Phillips 1964; Pereyra et al. 1969; Brodeur 1982). Brodeur (1982) examined seasonal changes in the diets of *S. flavidus* and *S. pinniger*, and found that food consumption declined during winter in *S. pinniger*, but not in *S. flavidus*. However, Carlson and Barr (1977) found a pronounced decline in activity during winter in *S. flavidus* off Alaska, suggesting seasonal changes in feeding. This hypothesis can be examined with concurrent data on food consumption and fat volume. It is not mutually exclusive with other functions of fat reserves, since some fat could also be used for migration, nourishment of embryos, or maturation of additional ova in multiple spawners.

The wintertime use of reserves for maintenance, however, is consistent with the overall pattern of long life and repeated reproduction in rockfish (as discussed also by Gunderson [1977]). As suggested by Slobodkin (1962) and Calow (1977), summertime fat deposition may exact a cost in current reproduction (if more gametes could be packed into rockfish abdomens) or in future increases in gamete capacity (through additional growth), but may help to ensure survival.

An interesting result of our study was the difference in magnitude of fat cycles among species, which was particularly evident in females. These differences are correlated with both the frequency of spawning and geographical distributions of the species. Females of *S. entomelas* and *S. flavidus* had fat cycles of high amplitude and volume, probably spawn only once a year (Westrheim 1975; Echeverria footnote 5), and have northerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). On the other hand, *S. paucispinis* and *S. goodei* had fat cycles of low amplitude and/or volume, spawn more than once a season, at least in southern California, and have southerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). The case with *S. pinniger* is unclear. Females seemed to have low-amplitude fat cycles, but the small sample and small sizes of females in the samples make conclusions tenuous. Echeverria (footnote 5) has some evidence for multiple spawning in *S. pinniger*. If so, its northerly distribution would be inconsistent with the pattern seen in the other species. We will restrict our discussion to the remaining four species, although further studies of *S. pinniger* may be instrumental in evaluating the suggestions we make below.

The small fat cycles of multiple spawners are probably not caused by their potentially greater reproductive output, since fat deposition stops long before the maturation of additional batches of ova. It seems more likely that the magnitude of the fat cycle, frequency of spawning, and geographical distribution are all related. Boehlert and Kappenman (1980) suggested that year-round spawning in southern populations of *S. diploproa* served to increase reproductive output in response to annual variation in the survival of planktonic larvae. Multiple spawning in southern populations and species may also be a response to the more even seasonal distribution of upwelling in southern vs. northern areas of the northeastern Pacific (Bakun et al. 1974; Parrish et al. 1981; Smith 1978), as it affects planktonic larvae. However, the more restricted upwelling season in northern waters may also lead to larger and better defined seasonal variation in the food supply of adults. A more pronounced summertime pulse of food may enable northerly species like *S. entomelas* and *S. flavidus* to store large amounts of fat. Similarly, a more pronounced decline in food during winter may make the accumulation of such reserves necessary, and preclude the maturation of additional batches of ova. On the other hand, a more even seasonal distribution of food in the south may enable southerly species like *S. paucispinis* and *S. goodei* to produce additional batches of ova during winter, and may also reduce the need for wintertime reserves. These suggestions are speculative, but it should be possible to compare the seasonal variation of food consumption in species with northern vs. southern distributions.

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[7] Hobson, E. S., and J. R. Chess. 1981. Seasonal patterns in trophic relationships of the blue rockfish, *Sebastes mystinus*. [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

In summary, we suggest that seasonal changes in the availability of food are rather important in the life histories of rockfish. The summer storage and winter use of fat reserves, in near synchrony with growth and decline of gonad volume, indicate a wintertime paucity of food that is compensated by the use of material that was stored at the expense of fecundity or growth. Further study of seasonal feeding, fat deposition, and reproductive cycles, categorized by size and sex, would be useful in evaluating this hypothesis. Further, geographical comparisons of these cycles may illuminate some causes of differences in the life histories of rockfishes.

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LITERATURE CITED

Adams, P. B.
1980. Morphology and distribution patterns of several important species of rockfish (genus *Sebastes*). Mar. Fish. Rev. 42(3-4):80-82.

Bagenal, T.
1978. Aspects of fish fecundity. *In* S. D. Gerking (editor), Ecology of freshwater fish production, p. 75-101. Blackwell Scientific Publications, Oxford.

Bakun, A., D. R. McLain, and F. V. Mayo.
1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish. Bull., U.S. 72:843-844.

Boehlert, G. W., and R. F. Kappenman.
1980. Latitudinal growth variation in the genus *Sebastes* from the northeast Pacific Ocean. Mar. Ecol. Prog. Ser. 3:1-10.

Boehlert, G. W., and M. M. Yoklavich.
1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. (Woods Hole) 167:354-370.

Bolin, R. L., and D. P. Abbott.
1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Oceanic Fish. Invest. Rep. 9:23-45.

Brodeur, R. D.
1982. Food habits, dietary overlap and gastric evacuation rates of rockfishes (Genus *Sebastes*). MS Thesis, Oregon State Univ., Corvallis, 102 p.

Calow, P.
1977. Ecology, evolution and energetics: a study in metabolic adaptation. Adv. Ecol. Res. 10:1-62.

Calow, P., and J. B. Jennings.
1977. Optimal strategies for the metabolism of reserve materials in microbes and metazoa. J. Theor. Biol. 65:601-603.

Carlson, H. R., and L. Barr.
1977. Seasonal changes in spatial distribution and activity of two species of Pacific rockfishes, *Sebastes flavidus* and *S. ciliatus* in Lynn Canal, southeastern Alaska. Mar. Fish. Rev. 39(3):23-24.

Dawson, A. S., and A. S. Grimm.
1980. Quantitative seasonal changes in the proteins, lipid and energy content of the carcass, ovaries and liver of adult female plaice, *Pleuronectes platessa* L. J. Fish Biol. 16:493-504.

Delahunty, G., and V. L. de Vlaming.
1980. Seasonal relationships of ovary weight, liver weight and fat stores with body weight in the goldfish, *Carassius auratus* (L.). J. Fish Biol. 16:5-13.

Derickson, W. K.
1976a. Introduction to the symposium: lipids in animal life histories. Am. Zool. 16:629-630.
1976b. Lipid storage and utilization in reptiles. Am. Zool. 16:711-723.

de Vlaming, V. L., G. Grossman, and F. Chapman.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31-39.

Diana, J. S., and W. C. MacKay.
1979. Timing and magnitude of energy deposition and loss in the body, liver, and gonads of northern pike (*Esox lucius*). J. Fish. Res. Board Can. 36:481-487.

Dotson, R. C.
1978. Fat deposition and utilization in albacore. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 343-355. Acad. Press, N.Y.

Foltz, J. W., and C. R. Norden.
1977. Seasonal changes in food consumption and energy content of smelt (*Osmerus mordax*) in Lake Michigan. Trans. Am. Fish. Soc. 106:230-234.

Glebe, B. D., and W. C. Leggett.
1981a. Temporal, intra-population differences in energy allocation and use by American shad (*Alosa sapidissima*) during the spawning migration. Can. J. Fish. Aquat. Sci. 38:795-805.
1981b. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. Can. J. Fish. Aquat. Sci. 38:806-820.

Guillemot, P. J.
1982. Seasonal cycles of fat content and gonad volume in species of northern California rockfish (Scorpaenidae: *Sebastes*). MA Thesis, San Francisco State Univ., San Francisco, 167 p.

Gunderson, D. R.
1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region, and their response to the fishery. Fish. Bull., U.S. 75:369-403.

Gunderson, D. R., P. Callahan, and B. Goiney.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74-79.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42 (3-4):2-16.

Helvey, M.
1982. First observations of courtship behavior in rockfish, genus *Sebastes*. Copeia 1982:763-770.

Hunter, J. R., and R. Leong.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

Iles, T. D.
1974. The tactics and strategy of growth in fishes. *In* F. R. Harden-Jones (editor), Sea fisheries research, p. 331-345. Wiley, N.Y.

Kleinbaum, D., and L. Kupper.
1978. Applied regression analysis and other multivariable methods. Duxbury Press, North Scituate, Mass., 556 p.

Lasker, R.
1970. Utilization of zooplankton energy by a Pacific sardine population in the California Current. *In* J. H. Steele (editor), Marine food chains, p. 265-284. Oliver and Boyd, Edinb.

Lasker, R., and P. E. Smith.
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.

Lawrence, J. M.
1976. Patterns of lipid storage in post-metamorphic marine invertebrates. Am. Zool. 16:747-762.

Love, M. S.
1981. Evidence of movements of some deepwater rockfishes (Scorpaenidae: genus *Sebastes*) off southern California. Calif. Fish Game 67:246-249.

Love, M. S., and W. V. Westphal.
1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. Fish. Bull., U.S. 79:533-545.

Love, R. M.
1970. The chemical biology of fishes: with a key to the chemical literature. Acad. Press, Lond., 547 p.

MacGregor, J. S.
1970. Fecundity, multiple spawning, and description of the gonads in *Sebastodes*. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 596, 12 p.

MacKinnon, J. C.
1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Board Can. 29:1749-1759.

Moser, H. G.
1967. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773-797.

Newsome, G. E., and G. Leduc.
1975. Seasonal changes of fat content in the yellow perch (*Perca flavescens*) of two Laurentian lakes. J. Fish. Res. Board Can. 32:2214-2221.

Parrish, R. H., C. S. Nelson, and A. Bakun.
1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1:175-203.

Patzner, R. A.
1980. Cyclical changes in weight and fat condition of the liver and their relationship to reproduction in the hagfish *Eptatretus burgeri* (Cyclostomata). Acta Zool. 61:157-160.

Pereyra, W. T., W. G. Pearcy, and F. E. Carvey, Jr.
1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. 26:2211-2215.

Phillips, J. B.
1957. A review of the rockfishes of California (family *Scorpaenidae*). Calif. Dep. Fish Game, Fish Bull. 104, 158 p.
1964. Life history studies on ten species of rockfish (Genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

Pierce, R. J., T. E. Wissing, J. G. Jaworski, R. N. Givens, and B. A. Megrey.
1980. Energy storage and utilization patterns of gizzard shad in Acton Lake, Ohio. Trans. Am. Fish. Soc. 109:611-616.

Roberts, D. A.
1979. Food habits as an ecological partitioning mechanism in the nearshore rockfishes (*Sebastes*) of Carmel Bay, California. MA Thesis, San Francisco State Univ., San Francisco, 74 p.

Robertson, O. H., and B. C. Wexler.
1960. Histological changes in the organs and tissues of migrating and spawning Pacific salmon (Genus *Oncorhynchus*). Endocrinology 66:222-239.

Shchepkin, V. Ya.
1971a. The dynamics of lipid composition in the Black Sea horsemackerel [*Trachurus mediterraneus ponticus* (Aleev)] in relation to maturation of the gonads and spawning. J. Ichthyol. 11:587-591.
1971b. Dynamics of lipid composition of the scorpionfish [*Scorpaena porcus* (L.)] in connection with maturation and spawning. J. Ichthyol. 11:262-267

Shevchenko, V. V.
1972. Dynamics of the content of dry fat-free residue and of lipid content in the body and organs of the North Sea haddock [*Melanogrammus aeglefinus* (L.)] in the course of growth and gonad maturation. J. Ichthyol. 12:830-837.

Shul'man, G. E.
1974. Life cycles of fishes: Physiology and biochemistry. Wiley, N.Y., 258 p.

Slobodkin, L. B.
1962. Energy in animal ecology. Adv. Ecol. Res. 1:69-101.

Smith, P. E.
1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-v Réun. Cons. int. Explor. Mer 173:117-127.

Sorokin, V. P.
1961. The redfish; gametogenesis and migrations of *Sebastes marinus* (L.) and *Sebastes mentalla* Travin. Rapp. P.-v. Réun. Cons. int. Explor. Mer 150:245-250.

Tyler, A. V., and R. S. Dunn.
1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. J. Fish. Res. Board Can. 33:63-75.

Westrheim, S. J.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

Wilkins, N. P.
1967. Starvation of the herring, *Clupea harengus* L.: Survival and some gross biochemical changes. Comp. Biochem. Physiol. 23:503-518.

Wootton, R. J., and G. W. Evans.
1976. Cost of egg production in the three-spined stickleback (*Gasterosteus aculeatus* L.). J. Fish Biol. 8:385-395.

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A Protocol for Designing a Sea Survey for Anchovy Biomass Assessment

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ABSTRACT

The objective of obtaining a representative sample of the adult northern anchovy population, for the purposes of determining reproductive status, is discussed. Several considerations affecting this objective are listed, including deterioration of tissue, vulnerability to sampling gear, geographic variability in reproductive behavior, logistic limitations, and secondary indicators of the presence of fish. The timing and duration of a survey, the laboratory equipment required, and potential problems are discussed. Specific specifications for a desired survey vessel are also outlined including sea day capability, gear operations, vessel speed, personnel, storage, work space, and cruise plan.

SEA SURVEY DESIGN AND METHODS

Collection Gear Requirements

The primary requirement for trawl collection gear is that it provides a representative sample of the adult anchovy population. Because it is the average fish that is of interest, rather than the average location, sampling density should parallel the density of fish. Thus, relatively fewer samples need be taken in sparsely populated waters near the edge of the range; however, these areas must be covered sufficiently well to confirm the extent of the range. Adult sampling should coincide as much as possible with the time and area of egg samples. Several considerations make this requirement difficult to achieve. These considerations include:

1) Fish must be preserved in a fresh condition so that histological criteria may be used to determine their reproductive status. The Southwest Fisheries Center currently requires that tissue be fixed within an hour of being caught, and this appears to be adequate. (Adult surveys conducted with a purse seiner off Peru extended this period to 2 h without adverse consequences; J. Alheit[2].) Because it is not possible to determine when a fish was captured, trawls must be of short duration so as to set and retrieve the net, subsample the catch, expose the gonads, and preserve the fish within the specified time period. The same must be required of alternative sampling gears such as purse seine or lampara nets.

2) Some portions of the adult population may be more vulnerable to capture than others; catches may vary with sampling gears, with time of day, and with reproductive status. In 1981, actively spawning female *Engraulis mordax* were oversampled with a trawl relative to females which had spawned the day before; purse seine catches, paired with the trawls, yielded equal proportions of active and postactive spawners. The sex ratio, determined from the trawl sample, was biased (towards males) only during the hours of spawning whereas the purse seine selectively caught females regardless of the time of day. The 1982 trawl survey caught equal proportions of active and postactive spawners although the sex ratio changed during the hours of spawning favoring the males (Picquelle and Hewitt, 1983). In contrast, a 1981 purse seine sample of Peruvian anchovy, *Engraulis ringens*, obtained off Peru oversampled actively spawning females as well as showed a diurnal pattern in the sex ratio of caught fish (Alheit et al., 1984). Furthermore, a comparison of the distribution of actively spawning females with a binomial distribution suggested that the fish were not independently distributed in the collections; fish which had spawned the day before appeared to be independently distributed. It was concluded from these observations that males and actively spawning females segregate out from other females during the peak hours of spawning at a depth (or an area) where they are more vulnerable to the trawl (Alheit et al., 1984). This behavior appears to begin early in the day before the ovaries hydrate and ends a few hours after spawning.

Bias due to gear selectivity, temporal or geographic distribution, or fish behavior should be watched for. Because it is not always evident, every set of adult collections should be checked for possible bias. Sampling gears and procedures should be modified so as to minimize potential bias. The ideal sampler is one that is invisible to the fish, to preclude avoidance, and one that samples through the entire vertical range of their distribution. If the source of bias cannot be eliminated, it may be corrected by use of appropriate availability factors and/or statistical stratification. If size of fish follows an oceanographic or geographic pattern, the samples must cover the range. For fishes which spawn very locally in time or space, representative sampling may be difficult, while for widely distributed spawners representative sampling may not be difficult to achieve.

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3) Spawning may occur in areas where it is difficult to sample the adults. These include the nearshore and other shallow water zones where there is not sufficient depth to fish a trawl or set a purse seine net. *Engraulis mordax* spawns in the nearshore zone with the same intensity as observed throughout its habitat (Hewitt and Brewer, 1983); however, the reproductive output of adults in this zone must be inferred because of the difficulty in sampling there. It may be necessary to choose a sampling gear, which can be deployed in shallow or obstructed areas (such as a lampara net), for those populations that deposit a large portion of their spawn in shallow waters

4) Time and personnel requirements must also be considered when selecting a sampling gear. As mentioned above, a gear should be eliminated if it cannot be set, retrieved, and the catch preserved in less than a specified time period. The vessels available and their speed of travel between stations may be determined by the choice of sampling gear. In general, a purse seine requires more people to deploy than does a trawl; however, there may be considerable variation between boats. One to two people are required to subsample and preserve the catch in addition to the personnel necessary to fish the gear.

Secondary information may be useful for improving sampling efficiency, but care must be taken not to cause unrepresentative sampling. For example, presence of eggs in the plankton tows indicates presence of fish, but absence of eggs does not imply absence of fish. Adult samples from areas of low spawning rates may be very important in obtaining a good biomass estimate. Secondary information may improve trawl success rates. Such information may include signs of fish encountered during recent survey operations, signs of predators, and results of other observers such as the fishery, airplane pilots, or other concurrent research cruises. If fish behavior is known, oceanographic information on water temperature, clarity, etc., may provide useful clues to presence and absence of fish.

It is highly recommended that adult collections be examined for evidence of avoidance and selectivity. In this regard, it is a good practice to sample the catch for age composition. This information may be used as additional criteria to compare gears, geographic areas, and time of day.

SURVEY TIMING AND DURATION

The timing of the survey should be based on biological information. The survey should be conducted during peak spawning activity of the adults. The number of samples required to estimate the spawning fraction increases exponentially as that fraction decreases (P. E. Smith[3]) so that the additional cost of sampling outside the spawning season rapidly becomes unacceptable. It is absolutely necessary that adult sampling be conducted simultaneously with egg sampling, either on the same vessel or on different vessels working in the same vicinity.

The duration of the survey depends on logistical considerations. These include area of the survey, desired sampling intensity, distance between stations and speed of the vessel, and fraction of the day available to conduct adult sampling. If more than one vessel is available, sampling may be conducted 24 hours/day, which would allow more stations to be occupied in the same amount of time. However, the fish may be less catchable during daylight hours, either because they are deeper or because they can better avoid the net. As with the choice of gear. a compromise must be made between quantity and quality of the data (i.e., precision and accuracy).

EQUIPMENT AND SUPPLIES

Adult sampling equipment can be divided into two general categories: Sampling gear and laboratory supplies. Sampling gear is usually specific to the vessel employed for the survey and is discussed below under "Vessel Requirements." Laboratory equipment refers to everything necessary to subsample the catch and preserve the specimens: buckets for subsampling, preserving solution, labels, data sheets, and specimen jars. Also useful are a small scoop, specimen jar rack, dissecting scissors, small spatula, forceps, and a hand digital logger with at least three registers (e.g., blood cell counter). The survey should be planned in enough detail to take the proper amount of supplies. Because space on a vessel is usually at a premium and because running short of supplies is also costly, it is recommended that extra supplies be kept onboard.

SOURCES OF ERRORS, BIASES, AND POTENTIAL PROBLEMS

The most serious source of bias is the selectivity of adult fish sampling gear. As discussed above, suspected biases should be investigated and, if necessary, changes should be made to the gear and/or sampling procedures. A representative sample is achieved when each adult fish has an equal probability of being caught by the sampler; if ripe females are more vulnerable to capture than the rest of the adult population or if fish were more able to avoid the net during certain times of the day, then a representative sample is not achieved, and this fact must be considered. In the survey for *Engraulis mordax*, where these problems were encountered, ripe females were eliminated from the calculation of the spawning fraction and adult sampling was conducted during only a portion of the day.

Error may be introduced when there is geographic heterogeneity in spawning and homogeneous sampling. Close examination of the results and postsurvey stratification, if indicated, is the most direct method of reducing this error. Error may also be introduced when subsampling the catch aboard ship (e.g., an inadvertent preference for large fish); this may be reduced by devising a systematic procedure for selecting fish. Finally, it is important to clean the net between sets; fish can get caught in the webbing and become part of the apparent catch of a subsequent set. Off California, pelagic red crabs sometimes contaminate the catch and abrade the fish; these fish cannot be distinguished from the residual of a previous trawl unless the net is thoroughly flushed between sets.

VESSEL REQUIREMENTS

Because the survey vessel is the most important piece of equipment to be specified, it is prudent to consider the requirements in some detail. The following subsections outline the minimum considerations. Additional specifications and detail in planning will aid in the conduct of the survey. It is impossible to prepare too much.

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[3] P. E. Smith, Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, pers. commun. Sept. 1983.

Sea Days Capability

The vessel must be able to take on sufficient provisions and fuel to conduct a major portion of the survey without returning to port. A minimum two-week capability should be required to maintain survey continuity and to obtain samples in a reasonably short period of time. Bear in mind that a port call involves travel time to port, time in port, and travel time back to the next station; delays in sampling can easily become longer than originally anticipated.

Gear Operations

The vessel should be equipped with the specified adult sampling gear rather than bringing new gear aboard. The gear should be clean and in good operating order. The vessel's crew should be proficient in deploying and retrieving the gear as well as repairing minor damage to the net without returning to port. If members of the scientific party will be required to help operate the gear, the number of people and their duties should be clearly specified.

The winch requirements (as outlined above for egg sampling) should be clearly specified and stressed as critical to the conduct of the survey. Other requirements include provisions for measuring the wire angle and washing down the net.

It is most important that any collection operations (egg or adult) which involve the cooperation of the crew and the scientific party be discussed thoroughly and even practiced before the survey begins.

Vessel Speed

Knowledge of the vessel's speed is a key element in the planning of a survey because a major portion of time is spent underway between stations. Speed will vary according to sea conditions and the loading of the vessel; however, a realistic estimate of the expected average speed is very useful. The survey may be planned first and a minimum vessel speed specified as a criterion for vessel selection.

Personnel

The primary requirement for the vessel personnel is that they be adequate in number and sufficiently skilled to accomplish the specified operations. Competence in navigation should be a major requirement; this not only involves human skill but the proper equipment as well. It should be specified that each station must be accurately located and that it is not sufficient to know only the vessel position relative to port or land. As noted above, vessel personnel should know how to operate and repair the adult sampling gear.

Supplies and Specimen Storage

The vessel must have adequate space dedicated to dry storage of sampling supplies and specimens. These requirements must be calculated from the survey plan and can be considerable, particularly for the adult fish specimens. In addition to dry storage, storage space on deck may be specified for sampling gear and freezer storage may be necessary for some specimens.

Laboratory and Work Space

The vessel must have a covered space, well lit and well ventilated, that can be dedicated for use in processing specimens; running water and a drain are essential. Sufficient work space must exist on deck to store and deploy the egg sampler and the adult sampler, to remove their catches, and to subsample in the case of adult catches.

CRUISE PLAN AND WORK SCHEDULES

A cruise plan, distributed to all personnel involved (vessel crews and scientific parties) greatly increases the chance for a successful survey. Such a plan should include a brief statement of the cruise objectives, schedule of port calls, map of the stations and the order in which they are to be occupied, activities to be accomplished at each station, list of the personnel participating and those in charge, and a list of the equipment necessary to accomplish the objectives.

Work schedules should also be made and distributed prior to the cruise. These schedules alert participants as to when they will be working and what they will be doing so that they may be prepared. Careful thought should be given to how many people will be required on each vessel and whether the vessel can accommodate them. As an example, conducting operations 24 hours a day will require two or three work shifts for egg sampling, plus additional people for adult sampling. Each shift should have a designated leader, and one person, either from the crew or from the scientific party, should be in charge of adult sampling operations.

The value of a good plan cannot be emphasized enough. The plan should convey to all participants a clear, concise statement of what is to be accomplished on the cruise and how it is to be done. It should give the impression that a considerable amount of thought and preparation has already been done, and what remains is to carry out the plan. A survey cruise rapidly becomes tedious as the same operations are performed over and over; the plan helps people mark time and keep track of progress.

LITERATURE CITED

ALHEIT, J., V. H. ALARCON, and B. J. MACEWICZ.
1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25:43-52.

HEWITT, R. P., and G. D. BREWER.
1983. Nearshore production of young anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 24:235-244.

PICQUELLE, S. J., and R. P. HEWITT.
1983. The northern anchovy spawning biomass for the 1982-83 California fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 24:16-28.

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Comparison between Egg Production Method and Larval Census Method for Fish Biomass Assessment

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ABSTRACT

Ichthyoplankton abundance and production are related to the aggregate weight of spawning adults. The problem is first formulated in terms of annual production and fecundity. The abundance of northern anchovy larvae, used to index annual production, is related to the daily production of eggs. Advantages of the egg production method of assessing stock biomass are discussed.

INTRODUCTION

This final article discusses the general problem of relating ichthyoplankton data to the aggregate weight of spawning adults and reviews various solutions. The first section deals with the problem as traditionally formulated; that is, the annual production of eggs and larvae is related to adult biomass by annual fecundity. The second section reformulates the problem in instantaneous terms; that is, daily production and daily fecundity. The third section relates the two ichthyoplankton methods used to estimate the northern anchovy populations: The larval census method and the egg production method. The fourth section discusses the advantages of the egg production method.

ANNUAL PRODUCTION OF EGGS AND LARVAE

Although ichthyoplankton surveys have been conducted for many purposes—to detect unexploited fish stocks, to study development, biogeography and systematics of fishes, and to forecast future population growth—Hensen and Apstein (1897) initially proposed that the surveys be used to index the spawning population of adults. The idea was appealing because of the ease of sampling eggs and larvae relative to sampling adults. Ichthyoplankters are found in a restricted vertical range of the sea, they have no or very limited ability to avoid capture, and simple sampling gear can be employed which allows for increase in the density of observations.

The basic model relating the weight of the spawning population to production of eggs is (Saville 1964)

$$B = \frac{P}{F \times R}$$

where B is the weight of the spawning population, P is the annual production of eggs, F is the annual female fecundity on a weight basis (annual specific fecundity), and R is the female fraction of the population. Application of the method requires the ability to identify reproductive products of the target species and knowledge of their development rates, the geographic and seasonal extent of spawning, and the determination of batch size and number of batches spawned by a female each year.

The production of eggs can be estimated from egg abundance adjusted for their development time and the mortality suffered during this period (Sette 1943). Annual abundance is estimated by integrating individual observations over both the survey area and the spawning season. Several spatial integration procedures have been employed: Contouring the observations and measuring the topographic volume (Buchanan-Wollaston 1926; Van Cleve and Seymore 1953; Simpson 1959); summing of strata averages raised by strata areas (Sette 1943; Smith 1972; Berrien et al. 1981); and summing individual observations raised by the area that each observation represents (Sette and Ahlstrom 1948). The three methods yielded similar results when applied to surveys of Pacific sardine spawning by Sette and Ahlstrom (1948). Temporal integration has been accomplished by summing successive surveys weighted by the portion of the year that they represent (Sette and Ahlstrom 1948; Berrien et al. 1981) by measuring the area under the curve that describes the survey abundance by time of year (Simpson 1959; Bannister et al. 1974), integrating a normal curve scaled to describe the seasonal variation in spawning activity (Saville 1956), and summing quarterly estimates of average abundance (Smith 1

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(1964) advocated procedures which averaged over space and time because of the large (and unpredictable) variance between observations; he argued that estimates from integrating procedures did not have reliable estimates of variability and were not amenable to comparisons between years. Adjustments for development time and mortality can be made either before integration (e.g., Berrien et al. 1981), after integration (Sette 1943), or in a stepwise mixture of integration and adjustment (e.g., Bannister et al. 1974). Unless there is a strong correlation between abundance and rate of development or mortality within the survey area, the order of calculation should make little difference in the final estimate of annual egg production. If these factors are independent, then the various procedures discussed above are algebraically equivalent.

The most recent statistical advance in the description of ichthyoplankton surveys is the use of a weighted negative binomial distribution to describe the sample distribution (Zweifel and Smith 1981). Individual observations can be weighted for sampling bias and error (e.g., extrusion, avoidance, variations in the sample volume, and development rate), and the mean of the fitted distribution is an unbiased estimate of the production rate with a well-described error structure. Production is estimated by raising this mean over the space-and-time stratum encompassed by the observations. By fitting a weighted negative binomial to successive stage-specific sample distributions, an age-specific production curve may be derived (Hewitt 1982). Application of this procedure to the 30-yr time series of northern anchovy larvae surveys revealed a change in the microdistribution pattern (patch dispersal) of larvae as they grew and a change in the mortality rate with the level of egg production (Hewitt 1982).

Annual specific fecundity is estimated from knowledge of the number of eggs released per unit weight per spawning and the number of spawnings per year. Both factors can be affected by environmental conditions such as the amount, quality, and availability of food. For boreal species, for which spawning seasons tend to be distinct, short, and predictable, estimating annual specific fecundity may be less of a problem than for temperate and tropical populations, with protracted or even continuous spawning seasons. The problem of estimating annual specific fecundity may be sidestepped by assuming that production or abundance of eggs and larvae is proportional to the weight of the adult population; the proportionality constant is estimated by regressing the abundance of larvae on an independent estimate of population size (Smith 1972; Saville and Schnack 1981). Thus

$$B = k \times C \qquad \text{(Smith 1972)}$$

where C is the annual census of larvae and k is the proportionality constant. This procedure has come to be known as the Larval Census Method (Smith and Richardson 1977). Application of the method assumes that annual specific fecundity does not vary between years nor does the larval mortality rate (hence the use of larval abundance rather than production). To the extent that specific fecundity and larval mortality rate are independent of population size, violation of the assumptions introduces error but not bias in the estimate of the constant of proportionality.

The theory and conduct of ichthyoplankton surveys are discussed thoroughly in Smith and Richardson (1977); their bibliography (Smith and Richardson 1979) contains over 1,000 citations and is complete through 1973, including proceedings of the first Symposium on the Early Life History of Fish held at Oban, Scotland in 1973 (Blaxter 1974). The estimation of adult spawning stock size from egg and larval surveys is also discussed by Saville (1964, 1977), Hempel (1973), and Ulltang (1977). The proceedings of both symposia on the Early Life History of Fish (Blaxter 1974; Lasker and Sherman 1981) include several reports of estimates of stock size from ichthyoplankton surveys and provide a good introduction to a much larger body of literature.

DAILY PRODUCTION OF EGGS AND LARVAE

Development of the ability to determine the near-term reproductive status of a female allowed the stock-estimation problem to be reformulated in terms of parameters that were easier to measure. Hunter and Goldberg (1980) and Hunter and Macewicz (1980) developed criteria to describe the anchovy spawning cycle apparent in gonad tissue with a resolution of one day; i.e., it is possible to classify fish that were spawning on the day of capture, those that spawned the day previous to capture, those that spawned 2 days previous to capture, etc. Thus a direct measure of daily specific fecundity is possible as the product of the fraction of females spawning per day times the weight-specific batch fecundity. It is not necessary to integrate egg production over the spawning season because both fecundity and production can be expressed on a daily basis. The model relating the weight of the population to the daily production of eggs is (Parker 1980)

$$B = \frac{P_O}{F_s \times R}$$

where B is the weight of the spawning population, P_O is the daily production of eggs, F_s is the specific daily fecundity, and R is the female portion of the population. These parameters can be estimated from a representative sample obtained over the spawning habitat. For a fish that spawns continuously over a protracted spawning season (e.g., anchovy), the observations need not be made synoptically; rather, data collected over a 30-day cruise can be pooled without introducing large errors. This method has been used since 1980 to estimate the spawning stock of northern anchovy (Picquelle and Hewitt 1983a, b).

The production of eggs was estimated from the age-specific production curve (Fig. 1). The production rate of eggs at time zero (spawning) was raised over the survey area to estimate daily production by the population. The variance of this estimate was reduced using postsurvey stratification of the survey area.

Specific daily fecundity was estimated as the product of three parameters:

$$F_s = \frac{F \times S}{W}$$

where F is the average batch fecundity, S is the average fraction of adult females spawning per day, and W is the average weight of an adult female. These parameters were estimated from a sample of adult fish obtained concurrently with a sample of their eggs. The adult sample consists of ~100 trawl stations, and the egg sample ~1,000 plankton stations. Results of the four surveys conducted through 1983 are summarized in Table 1.

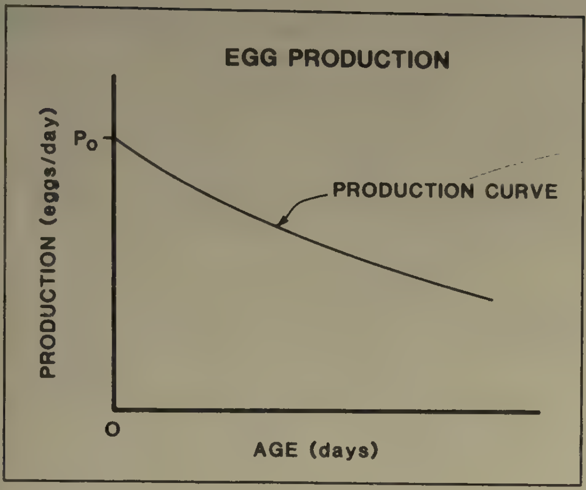

Figure 1.—Age-specific production curve of fish eggs. The curve is estimated from abundance-at-age data and the intercept is defined as the production rate (per unit area) of eggs at time zero (spawning).

RELATIONSHIP BETWEEN EGG PRODUCTION AND LARVAL CENSUS

The standing stock of larvae results from the production of eggs modified by mortality. Eggs are spawned continually by the adult population; some of them hatch, some of the larvae survive to metamorphosis, and many more perish as eggs or larvae. The average abundance of eggs and larvae is the sum of this process over all ages; i.e., the area under the production curve (Fig. 2). Thus, egg production is proportional to the zero intercept of the production curve, and the larval census is proportional to the area below the production curve. Both are raised above the survey area for population estimates and have a constant relationship to the extent that mortality is constant. The annual northern anchovy larval census was the latter value summed over four quarters (Smith 1972).

The expected abundance of northern anchovy larvae is the integral of the larval production curve from the time of hatch to 30 days (the oldest age at which anchovy larvae are effectively caught). The larval production curve is an extension of the egg production curve, and this is the basis for an analytical connection between the two methods. The larval production curve may be parameterized as (Lo 1985; Hewitt and Brewer 1983)

$$P_t = P_h \left(\frac{t_h}{t}\right)^{\beta} \quad \text{for } t < t_h$$

where P_t is the production of t-day old larvae, t_h is the age at hatch, and β is the larval mortality coefficient which describes how rapidly survival improves with age. The egg production curve may be parameterized as (Picquelle and Hewitt 1983a)

$$P_t = P_O e^{-Zt}$$

Table 1.—Egg production estimates of northern anchovy spawning biomass (1980-83). C.V. = coefficient of variation (standard deviation/mean).

		1980[1,4]		1981 (Feb)[1,4]		1981 (Apr)[1,4]		1982[2,4]		1983[3,5]	
		Est.	C.V.	Est.	C.V.	Est.	C.V.	Est.	C.V.	Est.	C.V.
Daily egg production ($\times 10^{12}$ eggs/d)	P_O	26.34	0.111	20.96	0.101	12.59	0.087	13.51	0.237	17.25	
Fraction of mature females spawning/d	S	0.142	0.125	0.106	0.122	0.125	0.092	0.120	0.038	0.094	
Sex ratio of weight (females/total)	R	0.478	0.120	0.501	0.063	0.495	0.051	0.472	0.081	0.549	
Batch fecundity (no. eggs/batch)	F	7,751	0.075	8,329	0.052	8,846	0.045	10,845	0.047	5,297	
Average female weight ($\times 10^{-6}$ t)	W	17.44	0.055	13.37	0.039	16.20	0.029	18.83	0.019	11.20	
Daily population fecundity ($\times 10^{-6}$ eggs/day-ton)	$q = SRF/W$	30.28		33.03		33.84		32.53		24.35	
Spawning biomass	$B = P_O/q$	870	0.225	635	0.183	372	0.147	415	0.257	652	0.211

[1] Documented in Stauffer, G.D., and S. J. Picquelle (Unpubl. manuscr.) Egg production estimates of spawning biomass of the northern anchovy, *Engraulis mordax*, for 1980 and 1981. SWFC, La Jolla, CA.

[2] Documented in Picquelle and Hewitt (1983a).

[3] Documented in Picquelle and Hewitt (1983b).

[4] These surveys were conducted with a 333-μm mesh net estimated to retain 91% of the eggs. Original estimates were elevated by a factor of 1/0.91.

[5] Biomass estimate was actually calculated as the sum of three regional biomass estimates. Parameter estimates reported here are averaged over the entire survey area for comparison purposes. See Picquelle and Hewitt (1983b) for regional parameter estimates.

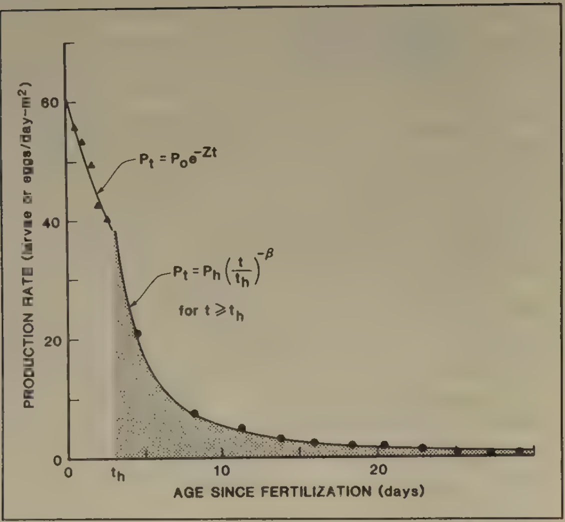

Figure 2.—Age-specific production curve of anchovy eggs and larvae. The average abundance of larvae is the shaded area under the larval production curve.

where Z is the instantaneous mortality coefficient, assumed to be constant over the incubation period. The production of eggs at the end of the incubation period may be substituted for the production of larvae at t_h.

The annual census of larvae averaged 2.12 times the standing stock during the spawning season (Stauffer and Picquelle 1980). The annual larval census also underestimated the true abundance of larvae because of losses due to extrusion and avoidance (Smith 1972; Lenarz 1972, 1973; Lo 1983). Thus, the annual census of larvae may be related to the daily production of eggs:

$$\hat{C} = 2.12(r)\, P_O e^{-Zt} \left(\frac{t_h}{\beta-1}\right)(1 - (t_h/30)^{\beta-1})$$

where r is the fraction of the larval population represented in an ichthyoplankton sample; r is a variable which is dependent on the size distribution of the larvae caught and the time of their capture. These relationships are developed in more detail by Stauffer (1983), Picquelle and Hewitt (1983a, b), and Lo (1985).

As was noted above, spawning biomass may be estimated using the larval census method by multiplying C times the constant of proportionality; this assumes no variability in reproductive output or early mortality. Spawning biomass may be estimated using the egg production method by dividing P_O by the daily specific fecundity; this procedure specifically accounts for variability in reproductive output and early mortality.

Results from the time series of egg production are listed below, together with projected larval census estimates. During the first two years larval surveys were conducted concurrently, and the measured larval census agreed well with the projected larval census.

YEAR	P_O ($\times 10^{12}$ eggs/d)	C ($\times 10^9$ larvae)	C ($\times 10^9$ larvae)
1980	26.34	17.22	18.10
1981 (Feb.)	20.96	35.12	28.58
(Apr.)	12.59	30.85	
1982	13.51	20.97	
1983	17.25	15.80	

The egg production surveys were conducted with the CalVET sampler described in Smith et al. (1985). The CalVET sampler has a 25-cm diameter mouth and is retrieved vertically to the surface from 70 m depth; it was designed to sample a small volume of water in a short period of time relative to the standard CalCOFI bongo sampler used to conduct larval surveys. The bongo sampler is a paired net with 60-cm diameter mouths and is retrieved obliquely to the surface from 210 m depth. Although the sampling gears are quite different, they yield consistent and compatible estimates of ichthyoplankton production.

These relationships may also be used to estimate historical egg production from the production curve of larvae and the abundance of eggs (Lo 1985). MacCall and Methot (1983) assembled the various measures of anchovy spawning biomass (egg production, back-projected egg production, acoustic surveys, and aerial spotter logs); they used acoustic and aerial data to fill in missing ichthyoplankton survey years and scaled the measures to the recent (1980-82) egg production estimates of biomass. The resulting 30-yr time series is the basis for a population model used to manage the harvest of anchovy (Pacific Fishery Management Council 1983).

ADVANTAGES OF THE EGG PRODUCTION METHOD

The egg production method is based on a model which uses instantaneous rates (daily egg production and daily specific fecundity). As such, a great economy is realized relative to annual estimates, because the necessary field data can be obtained on a single cruise. In the case of anchovy, at least four surveys were required to define the annual spawning activity (Smith 1972). Thus a major advantage to the egg production method is the relatively low cost of collecting field data.

The egg production method is also more precise than other ichthyoplankton methods. Early mortality and adult reproductive output are both measured rather than assumed or extrapolated from other observations. The extrapolated estimates may be accurate but they have a finite error associated with the estimation process that is eliminated when these parameters are measured directly. In the case of anchovy, the egg production method is also probably more accurate than the larval census method (Picquelle and Hewitt 1983a). This is because of inaccuracies in estimating the proportionality constant between the annual census of larvae and the weight of the adult stocks.

The egg production estimate of spawning biomass can be broken down into several factors each of which can be estimated, with an associated variance, from a sample of the population. These variances, together with the covariance between the parameters, may be used to estimate the variance of the estimate of spawning biomass. This is not so easily done with estimates based on annual rates because certain factors must be estimated without an idea of their variance (e.g., the number of batches spawned per year). It is also possible to measure the real variance of the egg production estimate of spawning biomass by conducting multiple surveys during the same year as was done in 1981.

LITERATURE CITED

BANNISTER, R. C. A., D. HARDING, and S. J. LOCKWOOD.
1974. Larval mortality and subsequent year class strength in the plaice (*Pleuronectes platessa* L.). *In* J. H. S. Blaxter (editor), The early life history of fish, p. 21-37. Springer-Verlag, N.Y.

BERRIEN, P. L., N. A. NAPLIN, and M. R. PENNINGTON.
1981. Atlantic mackerel, *Scomber scombrus*, egg production and spawning population estimates for 1977 in the Gulf of Maine, Georges Bank and Middle Atlantic Bight. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:279-288.

BLAXTER, J. H. S. (editor).
1974. The early life history of Fish. Springer-Verlag, N.Y., 765 p.

BUCHANAN-WOLLASTON, H. J.
1926. Plaice-egg production in 1920-21, treated as a statistical problem, with comparison between the data from 1911, 1914 and 1921. Fish. Invest. Ser. 2 Mar. Fish., G.B. Minist. Agric. Fish. Food 9 (2).

ENGLISH, T. S.
1964. A theoretical model for estimating the abundance of planktonic fish eggs. Rapp. P.-v. Réun. Cons. int. Explor. Mer 155:174-182.

HEMPEL, G. (editor).
1973. Fish egg and larval surveys. FAO Fish. Tech. Pap. 122, 82 p.

HENSEN, V., and C. APSTEIN.
1897. Die Nordsee-Expedition 1895 des Deutschen see fischerei-vereins. Uber die eimenge de winter laichenden fische. Helgol. Wiss. Meeresunters. 2(2), 101 p.

HEWITT, R. P.
1982. Spatial pattern and survival of anchovy larvae: Implications of adult reproductive strategy. Ph.D. thesis, Univ. Calif. San Diego, 187 p.

HEWITT, R. P., and G. D. BREWER.
1983. Nearshore production of young anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 24:235-244.

HUNTER, J. R., and S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., and B. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.

LASKER, R., and K. SHERMAN (editors).
1981. The early life history of fish: Recent studies. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178, 607 p.

LENARZ, W. H.
1972. Mesh retention of larvae of *Sardinops caerulea* and *Engraulis mordax* by plankton nets. Fish. Bull., U.S. 70:839-848.
1973. Dependence of catch rates on size of fish larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:270-275.

LO, N. C. H.
1983. Re-examination of three parameters associated with anchovy egg and larval abundance: Temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo. TM-NMFS-SWFC-31, 33 p.
1985. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951-82. Fish. Bull., U.S. 83:137-150.

MacCALL, A. D., and R. D. METHOT.
1983. The historical spawning biomass estimates and population model in the 1983 anchovy fishery management plan. Natl. Mar. Fish. Serv., NOAA, Southw. Fish. Cent. Admin. Rep. LJ-83-17, 53 p.

PACIFIC FISHERY MANAGEMENT COUNCIL.
1983. Northern anchovy fishery management plan. Pac. Fish. Mgmt. Counc., Portland, OR 97201.

PARKER, K.
1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78:541-544.

PICQUELLE, S. J., and R. P. HEWITT.
1983a. The northern anchovy spawning biomass for the 1982-83 California fishing season. Calif. Coop. Ocean Fish. Invest. Rep. 24:16-28.
1983b. Estimates of the spawning biomass of the northern anchovy for the 1983-84 California fishing season. Natl. Mar. Fish. Serv., NOAA, Southw. Fish. Cent., La Jolla, CA, Admin. Rep. LJ-83-15, 40 p.

SAVILLE, A.
1956. Eggs and larvae of haddock (*Gadus aeglefinus* L.) at Faroe. Mar. Res. Dep. Agric. Fish. Scotl. 4.
1964. Estimation of the abundance of a fish stock from egg and larval surveys. Rapp. P.-v. Réun Cons. int. Explor. Mer 155:164-173.

SAVILLE, A. (editor).
1977. Survey methods of appraising fishery resources. FAO Fish. Tech. Pap. 171, 76 p.

SAVILLE, A., and D. SCHNACK.
1981. Some thoughts on the current status of studies of fish egg and larval distribution and abundance. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:153-157.

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 1: Early life history, including the growth, drift and mortality of the egg and larval populations. U.S. Fish. Wildl. Serv., Fish. Bull. 50:149-237.

SETTE, O. E., and E. H. AHLSTROM.
1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. J. Mar. Res. 7:511-542.

SIMPSON, A. C.
1959. The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. Fish. Invest. Ser. 2 Mar. Fish., G.B. Minist. Agric. Fish. Food 22(7), 111 p.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

SMITH, P. E., and S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larval surveys. FAO Fish. Tech. Pap. 175, 100 p.
1979. Selected bibliography on pelagic fish egg and larval surveys. FAO Fish. Circ. 706, 97 p.

SMITH, P. E., W. FLERX, and R. HEWITT.
1985. The CalCOFI vertical egg tow (CalVET) net. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 27-32. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

STAUFFER, G. D.
1983. Calibration of northern anchovy spawning biomass estimates derived by egg production and larval census methods. Calif. Coop. Oceanic Fish. Invest. Rep. 24:11-15.

STAUFFER, G. D., and S. J. PICQUELLE.
1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. Natl. Mar. Fish. Serv., NOAA, Southw. Fish. Cent. Admin. Rep. LJ-80-09, 41 p.

ULLTANG, O.
1977. Methods of measuring stock abundance other than by the use of commercial catch and effort data. FAO Fish. Tech. Pap. 176, 23 p.

VAN CLEVE, R., and A. H. SEYMORE.
1953. The production of halibut eggs on the Cape St. James spawning bank off the coast of British Columbia 1935-46. Rep. Int. Pac. Halibut Comm. 19, 44 p.

ZWEIFEL, J. R., and P. E. SMITH.
1981. Estimates of abundance and mortality of larval anchovies (1951-75): Application of a new method. Rapp. P.-v. Réun Cons. int. Explor. Mer 178: 248-259.

REACTION OF DOLPHINS TO A SURVEY VESSEL: EFFECTS ON CENSUS DATA

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ABSTRACT

A field experiment is described in which a helicopter was used to observe the efficiency of shipboard line-transect sampling of dolphin populations in the eastern tropical Pacific Ocean. Nineteen dolphin schools were tracked; 13 of these were detected by observers aboard the ship and 5 of these reacted to the approach of the ship by altering the direction and/or the speed of their movement; however, only 1 school reacted prior to shipboard detection. The results suggest that dolphin schools only occasionally react to the approach of a survey vessel prior to their detection by shipboard observers and that the use of a monotonically decreasing detection function is adequate to minimize bias. Aerial and shipboard estimates of school size and species composition for six schools compared favorably.

The Marine Mammal Protection Act of 1972 prohibits the harvest of marine mammals and specifies that the Federal Government may issue permits for their take only under special circumstances. One such circumstance involves the incidental kill of dolphins associated with the yellowfin tuna fishery in the eastern tropical Pacific Ocean. Before issuing the permits, the government must first certify the viability of the affected dolphin populations. To meet this requirement, scientists at the Southwest Fisheries Center define stocks and monitor their population demography, reproductive output, and abundance.

The vital statistics are derived primarily from specimens obtained from the tuna fishery. However, to estimate abundance, surveys are conducted using ships and aircraft independently of the fishery. The surveys, using line-transect methods (Burnham et al. 1980), have yielded estimates of the density of dolphins in the eastern tropical Pacific Ocean (Holt and Powers 1982). A critical assumption in the application of the method is that the animals do not move, in reaction to the observer, prior to their detection. In practice, a detection function, which is relatively insensitive to nonrandom movement, is used to describe the probability of observing a school of dolphins given its position relative to the observer's transect. A field experiment was designed with the following objective:

1) Test the assumption that the animals do not alter their movement in reaction to the approach of a survey vessel *prior* to shipboard detection.

During a survey the unit of observation is a school of dolphins. In addition, species composition and the number of individual animals in a school (school size) are estimated. Surveys routinely collect information to determine the precision of these estimates by recording independent observations of several observers; however, determining their accuracy is more difficult and attempted less often (Holt and Powers 1982). Six schools were closely approached and observed from both an aircraft and a ship with the following objective:

2) Compare shipboard and aerial estimates of school size and species composition.

Although not an absolute determination of accuracy, the comparison yielded estimates from two very different viewpoints (high-altitude plan view versus low-altitude profile view).

A similar experiment was conducted using the NOAA Ship *Surveyor* and a ship-supported helicopter in 1977 (Au and Perryman 1982). They observed the reaction of eight dolphin schools to the approach of a ship; all eight schools swam away from the projected trackline of the ship. Au and Perryman also suggested that, in some cases, avoidance began beyond the visual range of shipboard observers. The present study was intended to collect additional data under a wider variety of conditions.

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METHODS

The experiment was designed to observe the efficiency of shipboard survey operations by using a helicopter to track dolphin schools before, during, and after shipboard detection. This approach was an enhancement of the design employed by Au and Perryman (1982) which focused only on the behavior of the dolphins. A simulated survey operation was included in the experiment for the following reasons:

1) It was not reasonable to assume that movement of a dolphin school and the probability of detecting it are unrelated (i.e., it may be easier to see a school in full flight than one at rest). Therefore, associated data on movement and shipboard detection were collected for each school.
2) It was necessary to separate random movement from directed movement toward or away from the survey vessel. To do so unambiguously, the ship could not be directed toward a school detected by the helicopter, but rather had to continue searching along a predetermined transect.

From the experience gained on the 1982 survey (Holt 1983), we expected 80% of the sighting cues to be within 3 nmi of the transect line and <5 nmi ahead of the vessel. Furthermore, the Au and Perryman observations on eight schools suggested that dolphins may react to a ship 6 nmi away. With these considerations and prior experience in mind, the following field procedure was employed.

The ship proceeded at 12 kn in a direction selected so as to minimize glare from the sea surface. Two observers maintained constant watch through 25 power binoculars, mounted on the port and starboard sides of the flying bridge (11 m above the water); search patterns extended from the bow to the beam of the ship on each side. Records were kept of searching effort and sighting details. With the exception of selecting the transect direction, these are the same methods employed during previous dolphin surveys (e.g., Holt and Powers 1982). The helicopter searched a distance of 8 to 12 nmi ahead of the ship and 2 nmi to either side of the transect line, at right angles to the direction of the ship's travel (Fig. 1). Search altitude was 1,200 ft and speed was 60 kn. When a school was sighted by the helicopter, shipboard radar tracking began. The observers on the flying bridge were not aware of a track in progress until its termination. Schools were tracked for about an hour's time until one of three events occurred: 1) the school passed abeam of the ship; 2) the school passed beyond the visual range of shipboard observers; or 3) the aerial observers lost sight of the school and had to terminate the track prematurely; in all of the latter cases the presence of the animals was obscured by deteriorating sea state.

During a track, the helicopter was positioned over the school at a minimum altitude of 1,200 ft (370 m); the radar range and bearing to the helicopter were determined from the approaching survey vessel about every 4 min (an interval sufficient to record the appropriate navigational data and still provide continuity in the track). A transponder, mounted on the aircraft, facilitated accurate radar measurements. In addition, OMEGA navigation positions were recorded from dual systems aboard the helicopter and the ship. As the track progressed, field notes were taken on visual observations of school behavior and associated birds and fish. The tracking altitude appeared to

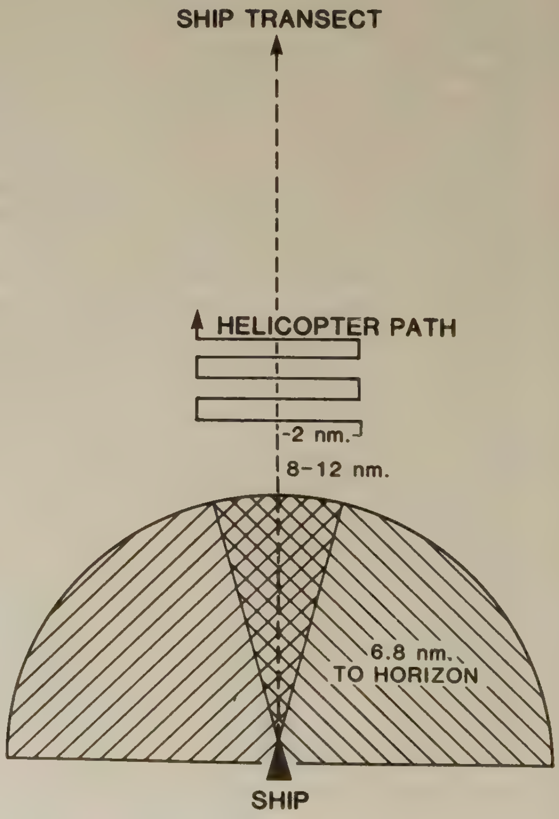


FIGURE 1.—Port and starboard search patterns (shaded areas) and path of helicopter (solid line) during transect (dashed line) surveys for dolphins.

be sufficient so as not to elicit a response from the animals. The dolphins appeared to be swimming calmly throughout the tracking; similar experience was reported by Au and Perryman (1982). It also placed the helicopter above the shipboard observers' vertical field of vision and therefore did not prematurely cue them on a school. Two oil drums were released and tracked at the beginning of the cruise to test the procedure: The resolution of radar measurements was 1-2° in bearing and 0.1 nmi in range; at 1,200 ft (370 m) altitude we were able to maintain visual contact with a 1 m object; and the shipboard observers were not aware of the helicopter until it was within 1 nmi of the ship, where the noise signaled its presence. Shipboard observers were questioned periodically throughout the experiment as to their cognizance of the helicopter; answers were always in the negative except when the binoculars were purposefully directed above the searching field. Observers were aware that looking for the helicopter would compromise the experiment and did not do so.

At the finish of a track, the helicopter descended to a lower altitude for additional photography and to estimate school size and species composition. The ship approached a limited number of schools to enable close-range shipboard estimates of the same school parameters. After school size and species composition were determined, normal survey operation resumed, with the helicopter searching ahead of the vessel and the shipboard observers actively scanning and recording search effort.

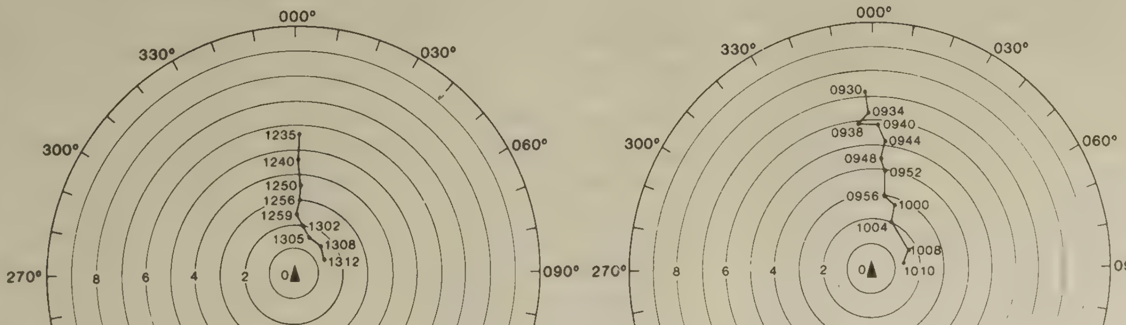
Relative motion radar plots were maintained. Apparent change in the relative direction of dolphin school movement was used as an indication of avoidance; field notes of aerial observations of behavior supplemented this information. The criteria defining reaction was a change of 30° or more in the direction of relative motion that was sustained over 2 or more subsequent fixes (Fig. 2).

The experimental design was opportunistic and only specifically designed to compare between a steam-powered survey vessel (NOAA Ship *Surveyor*) and a diesel-powered survey vessel (NOAA Ship *David Starr Jordan*). The experiment was conducted within a 100 square nmi area to the north and east of Clipperton Island (lat. 10°N, long. 110°W) during March and April 1983.[2] Observations were conducted with the *Surveyor* from 10 March through 17 March; the ship then ported at Manzanillo, Mexico, to take on fuel and subsequently met the *David Starr Jordan*, which had just completed a marine mammal survey[3] on 26 March at Clipperton Island. Observations were conducted in the same area with the *David Starr Jordan* until 7 April.

RESULTS

Avoidance

Tracks were started on a total of 26 dolphin schools, 5 in front of the *Surveyor* and 21 in front of



SCHOOL 8
Visual cue (birds) at 1306
Dolphins sighted at 1306

SCHOOL 23
Visual cue (birds) at 0926
Dolphins sighted at 0954

FIGURE 2.—Relative motion plots of dolphin school #8 and school #23. School #8 appeared to react to the approach of the ship; the sighting cue was reported after the dolphins' initial reaction. School #23 did not appear to react to the survey vessel.

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[2] Cruise Report NOAA Ship *Surveyor* Cruise RP-12-SU-83 dated May 24, 1983, on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[3] Cruise Report NOAA Ship *David Starr Jordan* Cruise DS-83-01 dated May 6, 1983, on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

the *David Starr Jordan;* a summary of the observations is listed in Table 1. Seven of the tracks were terminated prematurely, and of the remaining 19, 6 schools passed undetected by shipboard observers. These 6 schools did not appear to adjust their direction of movement in reaction to the survey vessel.

Of the 13 schools sighted by ship, 1 school altered its direction of movement in reaction to the approaching ship, prior to the detection of a sighting cue by the shipboard observers, and 12 schools did not appear to react before detection by the ship. One of the 12 schools was composed of rough toothed dolphins, *Steno bredanensis,* which are not a target of abundance surveys. Thus, from the results of this experiment, it is expected that 8% ($^1/_{12}$) of the target schools encountered on a survey will have moved (in reaction to the observer) prior to detection. This does not imply a corresponding degree of survey bias. Nonrandom movement, prior to detection, will alter the distribution of sighting distances and the detection function fit to the distribution; the survey will be biased to the extent that the functional form is sensitive to the data (see Discussion). Survey bias may also exist as a result of schools that react to the ship and are subsequently never seen by shipboard observers; if these schools would have been observed (the expectation is certain if they are on the transect line, less certain if they are off the line), then the bias is proportional to the fraction of schools that escaped detection. As stated above, no schools were observed to react to the ship and avoid detection.

The data suggest that dolphin schools may alter their direction of movement in reaction to the approach of a survey vessel. Thirty-eight percent ($^5/_{13}$) of the schools which were tracked by helicop-

TABLE 1.—Summary of dolphin school tracking data.

Vessel	School number	Beaufort sea state	Species composition		Number of individuals	Closest point of approach (nmi)	Reaction distance (nmi)	Radial sighting distance (nmi)	Relative bearing	Sighting cue	Interpolated radar position at time of sighting (range/bearing)
Surveyor	1	1	*Steno bredanensis*	100%	9	1.3	F^1	2.5	317°	animals	1.8/335°
	2	1	*Stenella attenuata* *S. longirostris*	50% 50%	175	7.0	F^1	F^2			
	3	3	*S. attenuata*	100%	53	2.5	F^1	F^2			
	4	5	Unidentified dolphins	100%	100	2.0	F^1	2.0	030°	splashes	4.0/032°
	5	5	Unidentified dolphins	100%	15	F^3					
Jordan	6	4	Unidentified dolphins	100%	22	F^3					
	7	4	Unidentified dolphins	100%	35	F^3					
	8	4	*S. attenuata* *S. longirostris* Unidentified dolphins	25% 5% 70%	300	1.5	2.5	1.5	024°	birds	1.6/030°
	9	4	Unidentified dolphins	100%	25	F^3					
	10	4	*S. attenuata* *S. longirostris*	20% 80%	150	0.5	1.7	6.0	003°	birds	6.3/002°
	11	4	*S. attenuata*	100%	25	5.0	F^1	6.8^4	023°	birds	7.2/019°
	12	4	*S. attenuata* *S. longirostris*	15% 85%	65	7.0	F^1	F^2			
	13	4	*S. attenuata* *S. longirostris*	65% 35%	175	1.3	2.2	6.8	356°	birds	6.2/357°
	14	4	*S. attenuata* *S. longirostris*	90% 10%	50	2.5	F^1	6.8^4	000°	birds	8.1/354°
	15	4	*Stenella* spp.	100%	150	F^3					
	16	4	*S. attenuata*	100%	35	1.2	1.5	6.0	357°	birds	7.0/359°
	17	3	Unidentified dolphins	100%	40	F^3					
	18	3	*S. coeruleoalba*	100%	160	F^3					
	19	3	*S. attenuata*	100%	45	3.0	F^1	F^2			
	20	0	*S. attenuata* *S. longirostris*	15% 85%	260	1.7	F^1	6.8^4	355°	birds	6.7/353°
	21	2	*S. attenuata* *S. longirostris*	91% 9%	230	6.4	F^1	F^2			
	22	1	*S. attenuata* *S. longirostris*	50% 50%	180	2.1	2.1	6.8^4	340°	birds	6.7/336°
	23	1	*S. attenuata* *S. longirostris*	50% 50%	155	1.5	F^1	6.8^4	004°	birds	8.0/357°
	24	1	*S. coeruleoalba*	100%	29	0.1	F^1	1.8	020°	animals	1.8/018°
	25	1	*S. attenuata* *S. longirostris*	40% 60%	410	2.0	F^1	4.0	015°	birds	5.0/010°
	26	1	*S. attenuata*	100%	85	3.0	F^1	F^2			

[1] School did not appear to react to the approach of the survey vessel.
[2] School passed undetected by shipboard observers.
[3] Track prematurely terminated.
[4] Cue observed on the horizon.

ter and detected by shipboard observers appeared to react to the ship. Spotted dolphins, *Stenella attenuata*, and spinner dolphin, *S. longirostris*, reacted at a distance of 0.5 to 2.5 nmi and were able to maintain a separation of 0.5 to 2.0 nmi from the ship; one school of striped dolphins, *S. coeruleoalba*, was successfully tracked and these animals stayed on a collision course with the ship until they were only a few hundred meters away. In all cases but one (school 8), the schools were detected by shipboard observers at distances far greater than the reaction distance.

None of the four dolphin schools successfully tracked in front of the *Surveyor* appeared to react to the approach of the ship. Five out of 15 schools appeared to react to the approach of the *David Starr Jordan*.

Estimates of School Size and Species Composition

Six schools were approached at close range by the *David Starr Jordan* so that shipboard observers could make estimates of school size and species composition using the same techniques that were used on previous abundance surveys. Estimates of school size and species composition were made independently by four to six shipboard observers and averaged, giving each an equal weight. These estimates compared favorably with estimates made by a single aerial observer stationed in the helicopter (Table 2). Shipboard estimates of school size ranged from 65 to 134% of the aerial estimates and averaged 101% (mean difference = 1.167; Pr = 0.713, paired t test of mean difference = 0); shipboard and aerial observers agreed on the species composition for all six schools compared, although there was some variation in the proportion assigned to each species.

DISCUSSION

The density estimator used in line-transect applications, formally derived by Burnham and Anderson (1976), and used to estimate the density of dolphin schools by Smith (1981) and Holt and Powers (1982), is:

$$\hat{D} = \frac{N\hat{f}(0)}{2L}$$

where $\hat{D}$ is the estimated density of dolphin schools in the survey area based on the number of schools observed, N, over transect length L. The function $f(x)$ is a probability density function fit to the observed perpendicular sighting distances and estimating its value at zero distance, $\hat{f}(0)$, is the critical concern in the application of line-transect methods (Burnham et al. 1980).

The frequency distribution of observed perpendicular sighting distances reflects both the detection abilities of the observer and the reactions of the observed (Burnham et al. 1980). Dolphin schools are more difficult to see with distance from the track line and avoidance, prior to detection, may cause fewer schools to be seen close to the track line and more schools to be seen further from the track line. The school that did move away from the transect line before shipboard detection (#8) would have been sighted at 0.1 nmi off the transect line if it had not altered the direction of its movement. Instead it was detected at 1.0 nmi off the transect line. If the sample size was larger, such information could be used to dissect the frequency distribution of perpendicular sighting distances into that component which is the result of decreasing visibility with distance from the transect line and that component which is the result of dolphin schools adjusting their natural spatial disposition

TABLE 2.—Comparison of shipboard and aerial estimates of dolphin school size and species composition.

	Vessel estimate				Helicopter estimate			
School number	Number of observers	Estimated number of individuals (standard error)	Species proportions (range)		Number of observers	Estimated number of individuals	Species proportions	
20	5	248 (24)	*S. attenuata*	0.14 (0.05-0.20)	1	260	*S. attenuata*	0.15
			S. longirostris	0.86 (0.80-0.95)			*S. longirostris*	0.85
22	4	241 (40)	*S. attenuata*	0.96 (0.90-1.00)	1	180	*S. attenuata*	0.50
			S. longirostris	0.04 (0.00-0.10)			*S. longirostris*	0.50
23	4	139 (20)	*S. attenuata*	0.62 (0.50-0.73)	1	155	*S. attenuata*	0.50
			S. longirostris	0.35 (0.22-0.50)			*S. longirostris*	0.50
			Unidentified	0.03 (0.00-0.12)				
24	6	36 (6)	*S. coeruleoalba*	1.00 (1.00-1.00)	1	29	*S. coeruleoalba*	1.00
25	5	393 (61)	*S. attenuata*	0.55 (0.40-0.70)	1	410	*S. attenuata*	0.40
			S. longirostris	0.39 (0.30-0.60)			*S. longirostris*	0.60
			Unidentified	0.06 (0.00-0.30)				
26[1]	5	55 (9)	*S. attenuata*	1.00 (1.00-1.00)	1	85	*S. attenuata*	1.00

[1] Not detected by shipboard observers while in survey mode; ship was directed to school by aerial observer.

in response to the ship. There are, however, other factors (such as glare and sea state) which are seldom constant long enough to allow for accumulation of a reasonably precise frequency distribution, such that the effects due to school movement would not be overwhelmed by the effects due to sighting conditions.

The results of this experiment suggest that 1) dolphin schools occasionally react to the approach of a survey vessel prior to their detection by shipboard observers and 2) the expected rarity of the event implies that a considerable amount of additional data would be required to quantify its effect.

Any directed movement prior to detection biases the frequency distribution of perpendicular distances and may bias the function, $f(x)$, fit to these data. In the absence of information regarding movement, Burnham et al. (1980) suggested choosing a function which is relatively insensitive to data contaminated by movement, i.e., a function that monotonically decreases with distance from the transect line. Their simulations suggest that in situations where "undetected movement is relatively minor, then use of an estimator based on a monotonically decreasing function will minimize bias in $\hat{D}$," (Burnham et al. 1980:130). The small sample size of the present experiment was sufficient to qualify undetected movement as relatively minor but not sufficient to quantify its effect on the distribution of perpendicular distances.

Although the work reported here was conducted in the same geographic area (Clipperton Island, lat. 10°N, long. 110°W) as the Au and Perryman (1982) observations, the two experiments are not strictly comparable. Au and Perryman used the ship and helicopter to search for schools and collected data on their reaction to the ship without regard to the effect on survey operations; in four of the eight schools they studied, the ship was turned toward the school during tracking. They were interested in describing the behavior of dolphin schools and combining the description with a search model to quantify survey bias. The present experiment did not assume that the two processes (reaction and detection) were independent and was less ambitious because there was no intention to generalize dolphin behavior. Indeed, the results presented here may only be relevant to this area and for these sighting conditions. Both the reaction distance and the sighting distance may be affected by environmental conditions and may vary between geographic areas with the degree of animal naivete.

The comparisons of aerial and shipboard results suggest that school-size estimates may be more reliable than those of species composition. Although neither observation platform can be considered to yield estimates without error, they do provide unique vantage points with very different views of the dolphin school. All shipboard observers, after exposure to observation conditions in the helicopter, agreed that they could more confidently estimate school size from the air than from a vessel. The helicopter provides an opportunity to observe the entire school over an extended period of time, making it easier to estimate that portion of the school which is submerged and not completely visible. Species proportions are more difficult to estimate and it is not clear which platform is better; indeed, in the case of school 22, all four shipboard observers reported similar proportions which were quite different than that estimated from the air. One explanation may be that it is more difficult to identify animals in plan view than in profile view; alternately, the fluid character of school structure may combine with the limited view of the school from a ship to preclude accurate estimates of species proportions; a third possibility is that both are inaccurate because of species-specific behaviors which make the animals less visible from above and/or the side.

Estimates of the density of dolphin schools are multiplied by the area of the survey, the average school size and the species proportions to estimate species abundances (Holt and Powers 1982). Because they affect the abundance estimates directly, biases in the latter two parameters may be more serious than the effect of school movement prior to detection. As an example, consider the six schools compared during this experiment: the average number of *S. attenuata* per school, estimated by shipboard observers, was 27% greater than that estimated from the helicopter data, the shipboard estimate of *S. longirostris* was 34% less than the helicopter estimates, and the estimate of *S. coeruleoalba* was the same for both platforms (Table 3). Although these differences should only be considered as variability between two estimates, they illustrate the direct dependence of abundance estimates on accurate estimates of species proportions. Avoidance affects density estimates less dramatically; its affect on $\hat{f}(0)$ may be somewhat offset by using a function that is relatively insensitive to predetection movement.

The application of line-transect methods requires that along the transect line all schools are seen with certainty. Any departures from the assumption of perfect detection, either because of

TABLE 3.—Average dolphin school composition.

	Vessel	Helicopter
Average school size (number of individuals)	185.3	186.5
Average species proportions		
S. attenuata	0.545	0.425
S. longirostris	0.273	0.408
S. coeruleoalba	0.167	0.167
Unidentified dolphin	0.015	
Average school composition[1]		
S. attenuata	102.5	79.3
S. longirostris	51.3	76.1
S. coeruleoalba	31.5	31.1

[1] Unidentified dolphins distributed proportionately among identified dolphins following Holt and Powers (1982).

movement or visibility effects, will introduce a negative bias in the density estimate that is proportional to the decrease in apparent density along the transect line (Smith 1979). The sample size was insufficient to test this assumption rigorously; only one school was observed on the transect line (school 14) and it was detected well beyond any of the reaction distances observed.

It is recommended that future fieldwork include additional comparisons of estimates of school size and species proportions. In addition, the assumption of certain detection along the transect line should be tested. Biases in school composition and detection on the transect line affect the abundance estimates directly and present a greater potential for inaccuracy than the degree of directed movement prior to detection observed during this experiment.

ACKNOWLEDGMENTS

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LITERATURE CITED

AU, D., AND W. L. PERRYMAN.
1982. Movement and speed of dolphin schools responding to an approaching ship. Fish. Bull., U.S. 80:371-379.

BURNHAM, K. P., AND D. R. ANDERSON.
1976. Mathematical models for nonparametric inferences from line transect data. Biometrics 32:325-336.

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE.
1980. Estimation of density from line transect sampling of biological populations. J. Wildl. Manage. Monogr. 72, 202 p.

HOLT, R. S.
1983. Report of eastern tropical Pacific research vessel marine mammal survey, May 15-August 3, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-29, 151 p.

HOLT, R. S., AND J. E. POWERS.
1982. Abundance estimation of dolphin stocks involved in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-23, 95 p.

SMITH, G. E. J.
1979. Some aspects of line transect sampling when the target population moves. Biometrics 35:323-329.

SMITH, T. D.
1981. Line transect techniques for estimating density of porpoise schools. J. Wildl. Manage. 45:650-657.

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THE 1984 SPAWNING BIOMASS OF THE NORTHERN ANCHOVY

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ABSTRACT

The 1984 estimate of the spawning biomass of the central subpopulation of the northern anchovy (*Engraulis mordax*) is 309,000 metric tons (MT). The estimate was obtained using the egg production method, where biomass is defined as the ratio of the daily production of eggs found in the sea and the daily specific fecundity of the population.

In 1984, as in 1983, the central subpopulation of northern anchovy was geographically distributed more offshore and northerly than in previous years. Spawning was apparent throughout the southern portion of the Southern California Bight as far south as the latitude of Ensenada; no spawning was evident within 50 km of the coast between San Diego and Ensenada. A small amount of spawning was detected adjacent to the coast between San Francisco and Monterey bays, California, and between Cape Colnette and Punta Baja, Baja California.

RESUMEN

El valor estimado de la biomasa de desove de la subpoblación central de la anchoveta del norte (*Engraulis mordax*), para 1984, es de 309.000 toneladas métricas (TM). Esta estimación se obtuvo utilizando el método de la producción de huevos, en el cual la biomasa se define como el cociente entre la producción diaria de huevos colectados en el océano y la fecundidad específica diaria de la población.

En 1984, al igual que en 1983, la subpoblación central de la anchoveta del norte estuvo distribuída más lejos de la costa y más al norte que en años anteriores. A lo largo de la parte sur de la Bahia del Sur de California y, hacia el sur, hasta la latitud de Ensenada, hubo señales de desove. No se observaron evidencias de aquél hasta 50 km mar adentro entre San Diego y Ensenada. Pequeñas cantidades de desove se detectaron en la vecindad de la costa entre las bahías de San Francisco y Monterey, California, y entre Cabo Colnette y Punta Baja, Baja California.

INTRODUCTION

This report documents the 1984 spawning biomass estimate of the central subpopulation of the northern anchovy (*Engraulis mordax*), as required by the most recent version of the Anchovy Management Plan adopted by the Pacific Fishery Management Council (PFMC 1983). In recent years the anchovy biomass has been assessed using two ichthyoplankton-based methods: larval census (Smith 1972; Stauffer and Parker 1980; Stauffer 1980; Stauffer and Picquelle 1981) and egg production (Parker 1980; Stauffer and Picquelle 1980; Picquelle and Hewitt 1983, 1984). The larval census method assumes a constant proportionality between larval abundance and spawning biomass, whereas the egg production method measures and incorporates variability in the proportionality parameter. Only the egg production method was used to calculate the 1984 spawning biomass.

The egg production method defines spawning biomass as the ratio of the daily production of eggs and the daily specific fecundity of the adult population. The daily production of eggs was derived from the density of eggs sampled in an ichthyoplankton survey, and from egg development rates as measured in the laboratory. The daily specific fecundity of the anchovy population was derived from adult fish sampled during a trawl survey, which yielded estimates of average female weight, batch fecundity, sex ratio, and the proportion of females spawning each night. The two samples were obtained concurrently on a survey conducted during the seasonal peak of spawning.

This report describes the survey results, the egg production estimate of spawning biomass, and the variance of the estimate.

DESCRIPTION OF THE SURVEY

The 1984 survey was conducted by the NOAA ship *David Starr Jordan* from February 7 through March 30, 1984. The survey area extended from San Francisco, California (38°N), to Punta Baja, Baja California (30°N), approximately 250 km offshore in the main spawning region. The station pattern (Figure 1) was occupied from north to south, with the exception of the area between San Diego and Punta Baja. During the last portion of the survey, five station lines, spaced 40 miles apart and extending offshore, were occupied while the ship worked to the south, and twelve inshore lines, spaced 10 miles apart, were occupied while northbound to San Diego.

Planktonic eggs were sampled at 938 stations (Figure 1) using a 25-cm-diameter net of 150-micron

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[Manuscript received February 7, 1985.]

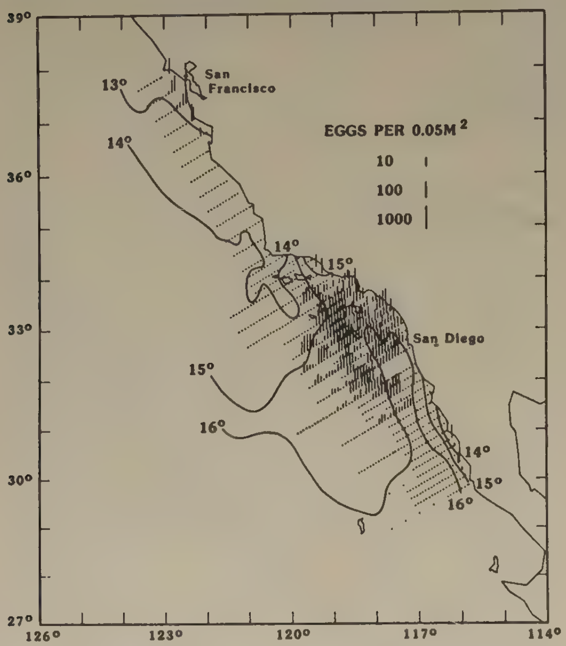

Figure 1. Geographic distribution of ichthyoplankton stations, anchovy eggs, and surface isotherms.

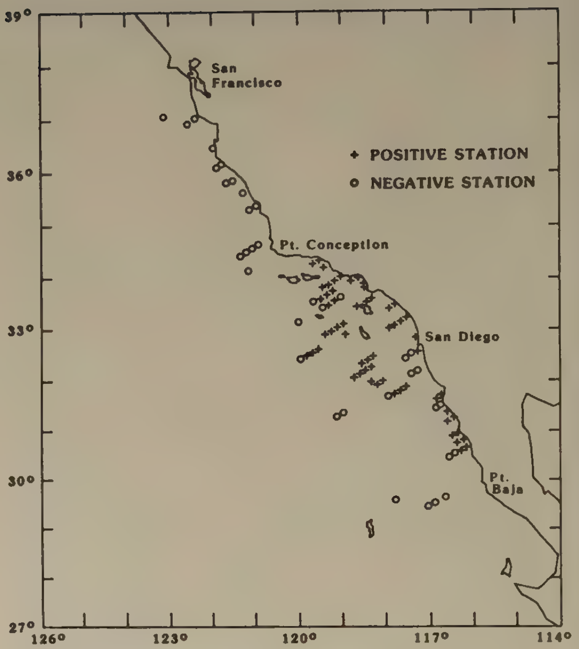

Figure 2. Geographic distribution of trawl stations.

mesh, retrieved vertically to the surface from a depth of 70 m; anchovy eggs were found in 384 of the 938 plankton tows. Planktonic samples were collected at all hours. Adults were sampled between 1800 and 0200 hours at 96 stations (Figure 2) using a 15-m² trawl with a 2-mm mesh liner; anchovies were caught in 66 of the trawl stations. (For a detailed description of field operations, see Cruise Report 8403-JD, dated May 31, 1984, William Flerx, Southwest Fisheries Center, La Jolla, California).

The geographic distribution of anchovy eggs was similar to that observed in 1983 and unlike previous years. In both 1983 and 1984 the range extended farther offshore, and a smaller proportion of eggs was taken off Baja California than in previous years. The distribution in 1984 was unique in that virtually no spawning was evident within 50 km of the northern coast of Baja California, although adult anchovies were caught in this area. Farther south and separate from the main spawning area, a few eggs were found very near shore between Cape Colnette and Punta Baja. Another inshore spawning area, separate from the main area, was detected extending from Monterey Bay to Point Reyes, north of the entrance to San Francisco Bay. This localized area of spawning has been evident in previous years. With the exception of northern Baja California, where the sampled fish were immature, the occurrence of positive trawls agreed well with the distribution of eggs. The egg and trawl surveys appear to have provided good sample coverage of the central subpopulation of northern anchovy in 1984.

There was an apparent correlation between the northern edge of spawning and the 14.5° isotherm; no correlation was evident along the southern boundary. A correlation between the range of the spawning population and temperature isotherms has been noted in previous years (Lasker et al. 1981; Picquelle and Hewitt 1983).

BIOMASS MODEL

The egg production estimate of anchovy spawning biomass and its variance is defined as:

$$B = P_o A \frac{k\ W}{R\ F\ S} \tag{1}$$

$$\mathrm{Var}\ (B) \cong B^2 \times \left\{ \frac{\mathrm{Var}\ (P_o)}{P_o^2} + \frac{\mathrm{Var}\ (W)}{W^2} + \frac{\mathrm{Var}\ (R)}{R^2} + \frac{\mathrm{Var}\ (F)}{F^2} + \frac{\mathrm{Var}\ (S)}{S^2} + 2 \left[\frac{\mathrm{Cov}\ (P_o W)}{P_o W} - \frac{\mathrm{Cov}\ (P_o R)}{P_o R} - \frac{\mathrm{Cov}\ (P_o F)}{P_o F} - \frac{\mathrm{Cov}\ (P_o S)}{P_o S} - \frac{\mathrm{Cov}\ (WR)}{WR} - \frac{\mathrm{Cov}\ (WF)}{WF} - \frac{\mathrm{Cov}\ (WS)}{WS} + \frac{\mathrm{Cov}\ (RF)}{RF} + \frac{\mathrm{Cov}\ (RS)}{RS} + \frac{\mathrm{Cov}\ (FS)}{FS} \right] \right\} \tag{2}$$

where B = spawning biomass in metric tons,
P_o = daily egg production rate in number of eggs per day per 0.05 m^2,
W = average weight of mature females in grams (g),
R = female fraction of the population by weight,
F = batch fecundity in number of eggs,
S = fraction of mature females spawning per day,
A = area of survey in units of 0.05 m^2, and
k = conversion factor from grams to metric tons (10^{-6} MT/g).

These expressions were developed by Parker (1980) and Stauffer and Picquelle (1980) and were used by Picquelle and Hewitt (1983, 1984).

DAILY PRODUCTION OF EGGS

The parameter $P_o A$, the daily production of eggs, is the survey area multiplied by the number of eggs spawned per night per unit area, averaged over the range and duration of the survey. Eggs were enumerated by stage of embryonic development, and were aged using temperature-dependent development rates and assuming that spawning occurs at 2200 hours each night. An exponential mortality model was fit to the egg data by assuming constant instantaneous rate of mortality. The daily egg production rate was estimated as the value of the predicted curve at the time of spawning.

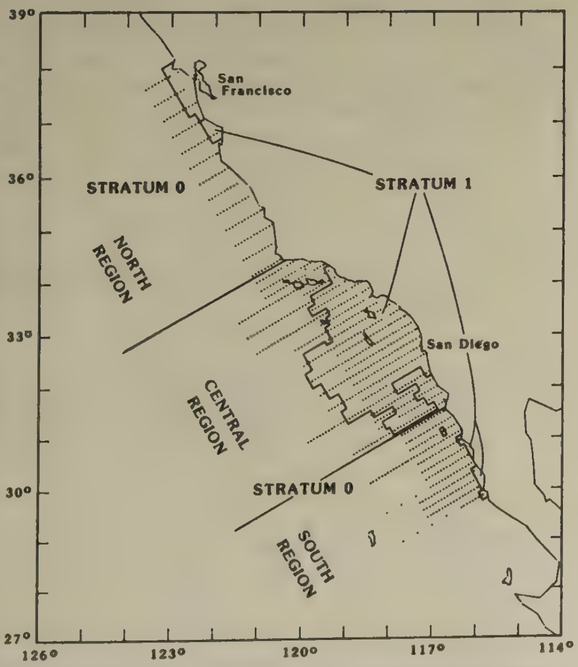

Figure 3. Subdivision of 1984 survey into strata (stratum 1 is the spawning area, and stratum 0 is devoid of eggs) and geographic regions (north, central, and south).

The egg counts were analyzed using a two-stage systematic sampling scheme (Picquelle and Hewitt 1983). First, each station was assigned a weight proportional to the area the station represents; second, the stations were stratified by location, where stratum 1 was defined as the geographic area of spawning, and stratum 0 was that area devoid of eggs (Figure 3). The exponential mortality model

$$P_{jt} = P_o^1 e^{-Zt} \tag{3}$$

was fit to the data by a weighted nonlinear least squares regression,

where P_{jt} = the number of eggs from the jth station of age t,
t = the age in days measured as the elapsed time from the time of spawning to the time of sampling at the jth station (because spawning occurs once a day and because the incubation period was 3 days or less, as many as 3 cohorts of eggs could be found at each station),
Z = the instantaneous rate of mortality on a daily basis, and
P_o^1 = the daily egg production rate in stratum 1.

The data and fitted curve are described in Figure 4. The daily egg production rate in stratum 0 is zero, and the daily egg production rate for the total survey area

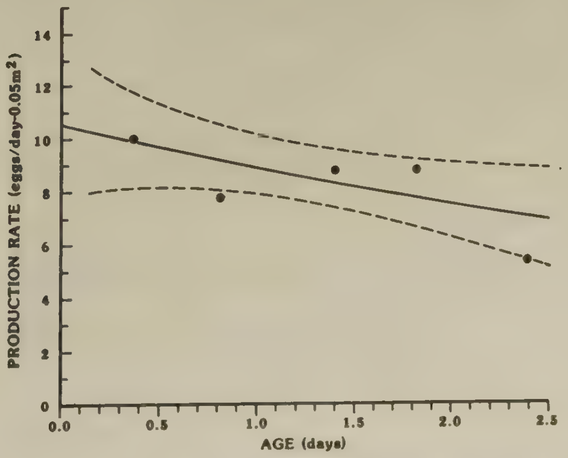

Figure 4. Egg production curve. The data is summarized as the mean abundance by half-day intervals, although the regression was fit to the individual data points. A 95% confidence region for the regression (broken line) is indicated.

TABLE 1
Parameters for Computing the Daily Production of Eggs

	Stratum 0	Stratum 1	Total survey
P_o	0	10.55	3.79
var (P_o)	0	1.66	0.60
Z	0	0.17	0.17
var (Z)	0	0.008	0.008
A	2.195×10^{12}	1.231×10^{12}	3.426×10^{12}
$P_o A$			12.98×10^{12}
var ($P_o A$)			7.02×10^{24}

and its variance (adjusted for postsurvey stratification; Jessen 1978) is:

$$P_o = \frac{A_1}{A} P_o' \tag{4}$$

$$\mathrm{Var}(P_o) = (1 + 1/n)[(A_1/A)\ \mathrm{Var}(P_o')] \tag{5}$$

where n = the total number of stations,
A_1 = the area of stratum 1, and
A = the total survey area.

The estimates for computing the daily production of eggs and their variances appear in Table 1.

ADULT PARAMETERS *W, F, S,* AND *R*

The parameters W, F, S, and R were estimated from a sample of adult anchovies collected by the midwater trawl. Each parameter was estimated by a weighted sample mean ($\bar{\bar{y}}$) with a weighted variance (Cochran 1963):

$$\bar{\bar{y}} = \sum_{i=1}^{n} \left(\frac{m_i}{\bar{m}n}\right) \bar{y}_i \tag{6}$$

$$\mathrm{Var}(\bar{\bar{y}}) = \frac{\sum_{i=1}^{n} \left[\left(\frac{m_i}{\bar{m}}\right)^2 (\bar{y}_i - \bar{\bar{y}})^2\right]}{n(n-1)} \tag{7}$$

where m_i = the number of fish subsampled from the ith trawl,
$\bar{m}$ = the average number of fish subsampled per trawl,
n = the number of positive trawls,
$\bar{y}_i$ = the average value for the ith trawl = $\sum_{j=1}^{m_i} y_{ij}/m_i$ and
y_{ij} = the observed value for the jth fish in the ith trawl.

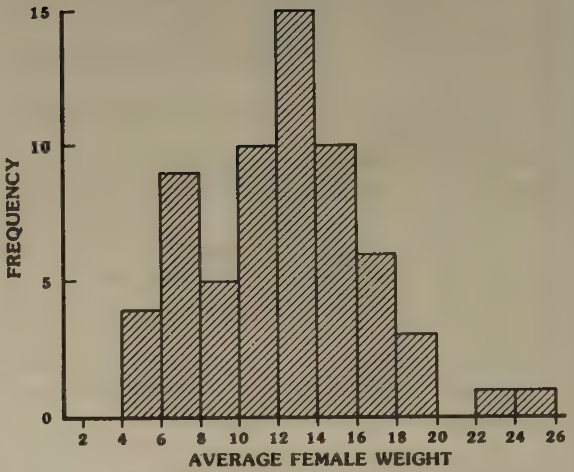

Figure 5. Frequency distribution of average mature female weight per trawl.

Average Female Weight

The average female weight was calculated using the above equations where $\bar{y}_i$ was the average female weight for the ith trawl. The desired subsample size was 25 fish from each trawl; however, this was not always possible for small trawl catches or for catches composed predominately of immature fish. The weight of females with hydrated eggs was adjusted for the extra weight of the fluid in their ovaries by measuring their ovary-free weight and estimating the whole-body weight of a female without hydrated eggs. The following regression, estimated from mature females without hydrated eggs, was used:

$$W = -0.176 + 1.06\, W^* \tag{8}$$

where W = estimated whole-body weight in grams, and
W^* = ovary-free weight in grams.

This regression had an $r^2 = 0.998$. The frequency distribution of average weight per trawl is described in Figure 5. the average female weight for the survey and its variance are listed in Table 2.

Batch Fecundity

Batch fecundity for each mature female was estimated from a regression of fecundity on ovary-free weight estimated from a sample of 75 hydrated females. The sample was selected so that the ovary-free weight distribution was similar to the ovary-free weight distribution of all the mature females (Figure 6). The regression model selected was:

$$F = -509 + 523\, W^* \tag{9}$$

TABLE 2
Estimates of Egg Production Parameters, Variances, and Coefficients of Variation

Parameter		Value	Variance	Coefficient of variation
Daily egg production (10^{12} eggs/day)	(P_o, A)	12.98	2.51	12.2%
Average female weight (g)	(W)	12.0170	0.21047	3.8
Batch fecundity (eggs)	(F)	5485.	96920.	5.7
Spawning fraction (day^{-1})	(S)	0.1597	0.00026	10.0
Female fraction	(R)	0.5820	0.00095	5.3
Daily specific fecundity (10^6 eggs/dayMT)		42.433		
Spawning biomass (MT)	(B)	306,000	2,547,706,812	16.5

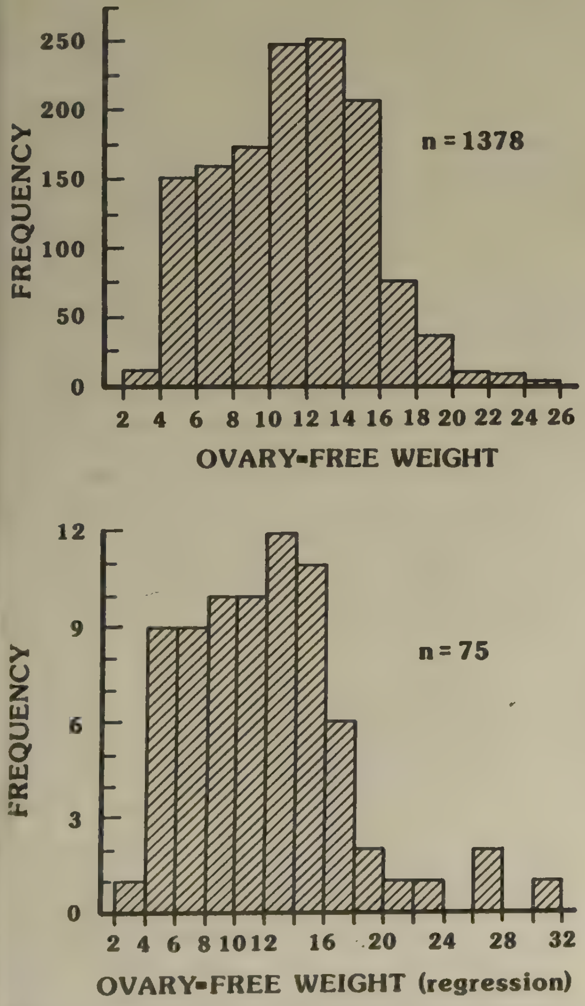

Figure 6. Frequency distributions of ovary-free weight for the entire survey (top) and for the females with hydrated ovaries used to estimate the batch fecundity/ovary-free weight regression.

where F = estimated fecundity for a female with W^* ovary-free weight (Figure 7). This regression had an $r^2 = 0.783$. Average batch fecundity for the survey was estimated using equation 6 where $y_{ij} = F_{ij}$ and the desired m_i was 25 mature females. The variance estimate (equation 7) was modified to include the extra source of variance from the batch fecundity/ovary-free weight regression (Draper and Smith 1966):

$$\mathrm{Var}(\bar{\bar{F}}) = \frac{\sum_{i=1}^{n} \left\{ \left(\frac{m_i}{\bar{m}} \right)^2 \left[\frac{(\bar{F}_i - \bar{\bar{F}})^2}{n-1} + \frac{S_h^2}{75} + (\bar{W}_i^* - \bar{W}_h^*)^2 \,\widehat{\mathrm{Var}}(b) \right] \right\}}{n} \tag{10}$$

where $S_h^2 = 2{,}291{,}706$ is the variance about the regression,
$\bar{W}_i^*$ = average ovary-free weight for the ith trawl,
$\bar{W}_h^*$ = 11.95 gr, average ovary-free weight of the 75 hydrated females used in the regression,
$\widehat{\mathrm{Var}}(b) = 1041$, variance of the slope of the regression, and
n = number of positive trawls.

The average batch fecundity for the survey and its variance are listed in Table 2.

Spawning Fraction

The spawning fraction, S, and its variance were estimated using equation 6 where $\bar{y}_i = S_i$ was the proportion of mature females in the ith trawl that spawned one night prior to capture (day-1 spawners). The desired m_i was 25 mature females. Based on previous experience (Picquelle and Hewitt 1983), it was suspected that females spawning on the night of capture (day-0 spawners) were oversampled by the trawl, thus biasing the proportion of day-1 spawners. To compensate for the potential bias, it was assumed

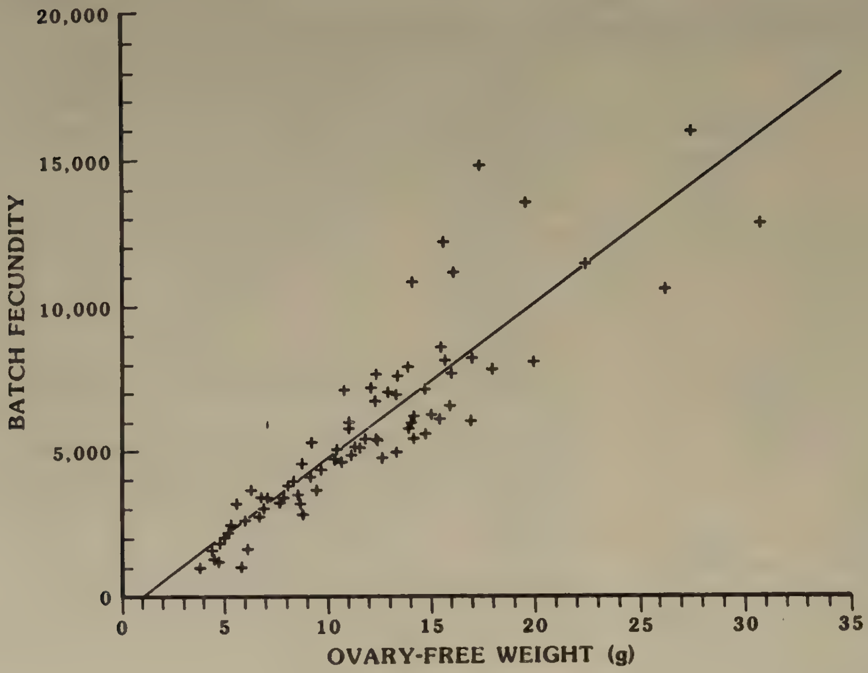

Figure 7. Linear regression of batch fecundity on ovary-free weight fit to 75 females with hydrated ovaries.

that the true proportion of day-0 spawners was equal to the observed proportion of day-1 spawners: the value of m_i in equations 6 and 7 is adjusted by deleting day-0 spawners from the sample and equating the number of day-0 spawners to the number of day-1 spawners, thus reducing the average subsample size, $\bar{m}$. The frequency distribution of the spawning fraction per trawl is described in Figure 8; the estimated spawning fraction for the survey and its variance are listed in Table 2.

Female Fraction

The female fraction, R, was measured as the fraction of females in the population by weight. Equations 6 and 7 were used by setting $\bar{y}_i = R_i$, where R_i is the estimated total weight of females in a subsample of 50 fish divided by the estimated total weight of the subsample; m_i was set equal to the total weight of the subsample. The average male and female weights for each trawl were estimated from 5 males and 25 females where the weight of any hydrated female was adjusted using equation 8. The frequency distribution of female fraction per trawl is described in Figure 9; the estimated female fraction for the survey and its variance are listed in Table 2.

BIOMASS ESTIMATE AND VARIANCE

The parameter estimates, their variances, coefficients of variation, and covariances are listed in Tables 2 and 3. The sample covariance terms were calculated only for the adult parameters. Because the daily egg production and the adult parameters were estimated from different samples, it was not possible to estimate their covariances, and they were assumed to be zero. The biomass estimate and its variance were

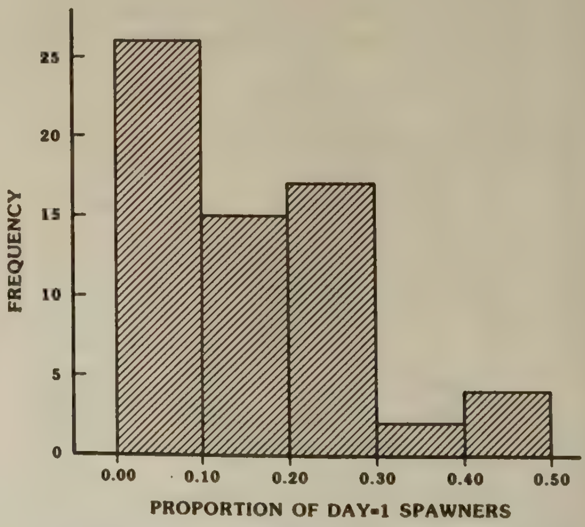

Figure 8. Frequency distribution of spawning fraction. Large portion of lowest class represents nonspawning fish from off northern Baja California.

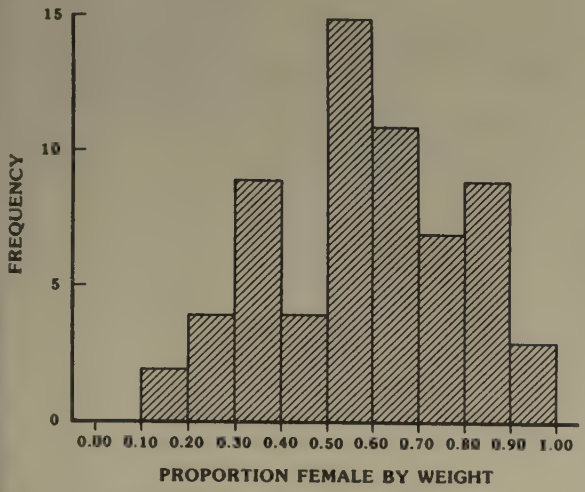

Figure 9. Frequency distribution of female fraction by weight.

TABLE 3
Covariances between Adult Parameters

	F	*S*	*R*
Female weight (*W*)	103.341133	0.00061	0.00085401
Batch fecundity (*F*)		0.30792	0.43871200
Spawning fraction (*S*)			−0.00009186
Female fraction (*R*)			

calculated using equations 1 and 2. The estimate of spawning biomass was 306,000 MT, with a standard error of 50,475 MT.

The survey was subsequently divided into three geographic regions (Figure 3) corresponding to the three distinct spawning areas. Daily egg production and daily specific fecundity were calculated for each region (Table 4). Because of the small number of trawls in the north and south regions, the estimate of the female fraction by weight (*R*) was unreliable; *R* was thus estimated for the entire survey and was assumed to be similar among regions. Since the parameter values for the three regions were very different (Table 4), homogeneity could not be assumed. Biomasses were calculated separately for each region and were summed to produce the final estimate of 309,000 MT. This estimate is not very different from the unregionalized estimate but should be more accurate. I was not able to produce a corresponding estimate of the total variance because some of the variances and covariances could not be calculated for the individual regions.

DISCUSSION

The 1984 estimate of the spawning biomass of the central subpopulation of the northern anchovy is less than half of the 1983 estimate (Table 5). Daily egg production by the population is down 25% from 1983, and the daily specific fecundity is up 75% from 1983. The daily specific fecundity is the highest ever estimated over the last five years and results from a high spawning fraction and a high female fraction by weight. Although the average female weight is slightly larger than the 1983 value, both years are low relative to the previous four surveys. Average batch fecundity is not unusual for the average female weight. This survey indicates that the spawning population comprises predominately small, young females with their center of distribution off southern California.

The geographical distribution of anchovies found in this survey agrees with an earlier report by the California Department of Fish and Game, (CDFG). K.F. Mais (Cruise Report 84-X-1, CDFG, Long Beach, California) conducted an extensive sonar and trawl survey from Point Conception, California, south to Punta Baja, Baja California, in February 1984. He reported that the anchovy central subpopulation was distributed more north and offshore than it was pre-

TABLE 4
Regional Estimates of Egg Production Parameters

Parameter		North region	Central region	South region
Daily egg production (10^{12} eggs/day)	($P_0 A$)	2.00	5.42	0.14
Average female weight	(*W*)	14.18	12.57	9.06
Batch fecundity	(*F*)	6584	5752	4043
Spawning fraction	(*S*)	0.1052	0.1748	0.0891
Female fraction	(*R*)	0.5820	0.5820	0.5820
Daily specific fecundity		28.44	46.57	23.15
Spawning biomass	(*B*)	70,300	234,400	4,000
Total biomass		308,700		

TABLE 5
Time Series of Egg Production Parameters

		1980	1981 (Feb.)	1981 (Apr.)	1982	1983	1984
Daily egg production (10^{12} eggs/day)	($P_o A$)	26.34	20.96	12.59	13.51	17.25	12.98
Average female weight	(W)	17.44	13.37	16.20	18.83	11.20	12.02
Batch fecundity	(F)	7,751	8,329	8,846	10,845	5,297	5,485
Spawning fraction	(S)	0.142	0.106	0.125	0.120	0.094	0.160
Female fraction	(R)	0.478	0.501	0.495	0.472	0.549	0.582
Daily specific fecundity (10^6 eggs/day-MT)		30.28	33.03	33.84	32.53	24.35	42.43
Spawning biomass (10^3 MT)	(B)	870	635	372	415	652	309
Calif. Dept. Fish and Game acoustic biomass estimate (10^3 MT)		498 to 598	493 to 591		233 to 247	461 to 504	479 to 560

vious to 1983. Mais estimated the biomass (including immature nonspawning fish) to be between 479,000 and 560,000 MT (Table 5). He also reported evidence of a relatively strong 1982 year class and weak 1981 and 1983 cohorts; fish of all ages were unusually small. Since 1980, acoustic abundance estimates have tended to be lower than those obtained by the egg production method (Table 5). This year's survey is unusual in that the acoustic survey results are substantially larger than the egg production method estimate. The young, nonspawning fish observed off northern Baja California, which were not included in the egg production method estimate, may account for some of this discrepancy.

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LITERATURE CITED

Cochran, W.G. 1963. Sampling techniques. John Wiley & Sons, New York, 413 p.

Draper, N.R., and H. Smith. 1966. Applied regression analysis. John Wiley & Sons, New York, 407 p.

Jessen, R.J. 1978. Statistical survey techniques. John Wiley & Sons, New York, 500 p.

Lasker, R., J. Peláez, and R.M. Laurs. 1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy, *Engraulis mordax*. Remote Sensing of Envir. 11: 439-453.

Parker, K. 1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish Bull., U.S. 78:541-544.

PFMC:Pacific Fishery Management Council. 1983. Northern Anchovy Fishery Management Plan. PFMC 526 S.W. Mill St., Portland, OR 97201.

Picquelle, S.J., and R.P. Hewitt. 1983. The northern anchovy spawning biomass for the 1982-83 California fishing season. CalCOFI Rep. 24: 16-28.

———. 1984. The 1983 spawning biomass of the northern anchovy. CalCOFI Rep. 25:16-27.

Smith, P.E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

Stauffer, G.D. 1980. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1979-80 fishing season. CalCOFI Rep. 21:17-22.

Stauffer, G.D., and K. Parker. 1980. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1978-79 fishing season. CalCOFI Rep. 21:12-16.

Stauffer, G.D., and S.J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. Southwest Fisheries Center Admin. Rep. LJ-80-09, 41 p.

———. 1981. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1980-81 fishing season. CalCOFI Rep. 22:8-13.

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Causes of mortality in young jack mackerel

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ABSTRACT: Field and laboratory experiments were conducted with the purpose of partitioning jack mackerel *Trachurus symmetricus* larval mortality into portions due to starvation and to predation. Field collections were made to determine larval condition, growth, net retention and production; laboratory experiments were conducted to determine growth and body shrinkage due to preservation treatment. Age-specific starvation and total mortality rates were estimated and predation was inferred as the difference between the two. In the offshore oligotrophic part of the spawning habitat, larvae suffered a high rate of mortality which rapidly declined as they developed. Predation was the major source of mortality of yolk-sac larvae. As the yolks were absorbed and the larvae began to feed, starvation became a significant source of mortality. As the larvae further developed, starvation rapidly declined and predation again became the dominant source of mortality, although at a much lower rate.

INTRODUCTION

Survival of young fish is limited by predation and starvation (Hunter 1984). Furthermore, these 2 sources of mortality may interact if starving larvae are more vulnerable to predation (Shepherd & Cushing 1980). The magnitude of mortality is influenced by endogenous factors (e.g. quality and quantity of yolk) and exogenous factors (transport, predator abundance and food supply). These factors act in concert on development and growth of young fish through the most hazardous phase of their life history. Above-average parental endowment and environmental conditions assure rapid, healthy growth and minimize mortality; on the other hand, poor parental endowment and adverse environmental conditions lengthen the period of extreme vulnerability. To link larval survival to recruitment of fish into the adult population, early mortality must be quantified. To understand the causes of mortality, a distinction must be made between that fraction due to starvation and that due to predation.

Earlier evidence points to predation as the major cause of larval mortality (Methot & Kramer 1979, O'Connell 1980, Ellertsen et al. 1981, Hunter 1984). In this field study we assess the mortality due to starvation and subtract it from total mortality rate to determine the rate of predation and the relative importance of these sources of mortality. We designed a field study to give us information on total mortality and starvation-induced mortality of young jack mackerel *Trachurus symmetricus*. We intensively sampled a small portion of jack mackerel spawning habitat, over a period of 4 d, off the coast of southern California. Total mortality of young jack mackerel was inferred from size-specific catch rates and the duration of growth within size categories (Hewitt 1981, Hewitt & Brewer 1983). Starvation mortality was determined using laboratory-developed histological criteria for characterizing jack mackerel condition (Theilacker 1978, 1981, in press). We then partitioned total mortality into the fraction due to starvation and the fraction due to predation.

METHODS

The sample area (Fig. 1) was chosen because it was well outside coastal and island influences and yet still within the spawning habitat of jack mackerel. In the first experiment, 3 ichthyoplankton samples were obtained over a close-spaced grid of stations: 1 sample was preserved in a formalin solution and used to estimate the size-frequency distribution of jack mackerel larvae; a second sample was preserved with Bouin's fixative and used for histological analysis of larval tissue condition; a third sample was preserved in alcohol and was the source of otoliths used to describe the growth of larvae. In 1983, a second collection was made using various net meshes for the purpose of quantifying the fraction of larvae extruded through the nets. Laboratory experiments were conducted to deter-

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mine the degree of larval body shrinkage that may be expected with various preservation treatments.

The size-specific larval catch curve was adjusted for extrusion losses and divided by the duration of growth to yield an age-specific production curve; the slope of this curve measures the total mortality rate. Growth of jack mackerel larvae was obtained from laboratory experiments (Theilacker 1978) and from daily growth increments in the otoliths of field-collected larvae. Larval condition and starvation mortality were estimated for each of 4 larval size categories (yolk-sac, < 3.5 mm, <4.0 mm and <4.5 mm). Field collections, estimation of total mortality, larval condition, growth, extrusion and shrinkage are described in more detail in the following sections.

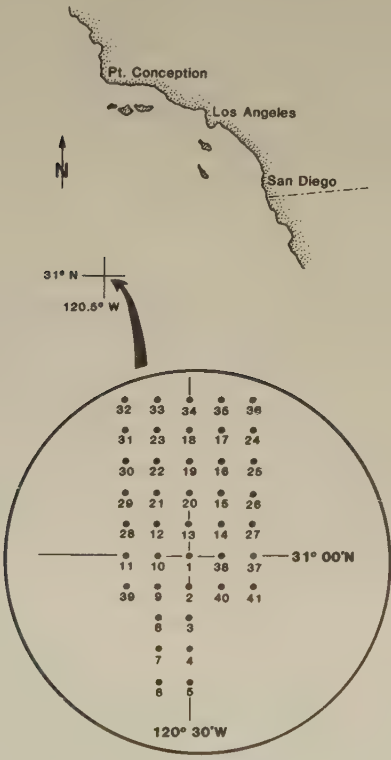

Fig. 1. The study area was a closed-spaced grid of stations 4 n mile apart and approximately 350 km southwest of San Diego, California

Field collections. In May 1980 jack mackerel eggs and larvae were sampled 350 km off the coast of California (Fig. 1) aboard the NOAA ship *David Starr Jordan.* A grid of 41 stations was established with 4 n mile spacing; stations were occupied over a 4 d period with 19 stations occupied twice to test for possible transport. At each station an oblique Bongo (60 cm mouth diameter) tow and an oblique 1 m ring tow, both fitted with 0.505 mm mesh nylon nets, were conducted (see Smith & Richardson 1977 for a description of these sampling gears). The Bongo tow yielded 2 samples; 1 was preserved in 10 % buffered formalin and the other was preserved in an 80 % alcohol solution. The 1 m ring tow sample was immediately preserved in Bouin's solution to avoid autolysis of larval tissues; after 2 d the Bouin's solution was replaced with a 70 % alcohol solution. In addition 28 vertical profiles of temperature and 3 of salinity profiles were obtained.

A second collection was made in April 1983 at 31°N, 121°W (approximately 30 n mile from the first collection) aboard the NOAA ship *Townsend Cromwell.* These catches were used to estimate extrusion of jack mackerel larvae through 0.333 mm and 0.505 mm mesh nets. Fifty oblique Bongo tows were conducted with paired nets made of 0.333 mm and 0.505 mm mesh nylon. Another 50 paired tows were conducted with nets made of 0.333 mm and 0.150 mm nylon mesh; these tows were made with a small-mouth (25.23 cm mouth diameter) apparatus (PAIROVET) retrieved vertically to the surface from a depth of 70 m. Both samples were preserved in a 10 % buffered formalin solution.

Total mortality. Jack mackerel larvae were sorted from the formalin-preserved plankton samples and counted by size. Catches were adjusted for extrusion losses using size-specific estimates of net retention (see 'Extrusion' section below).

To determine the mortality of the larvae we assumed that the size-specific abundance of larvae, measured at one time, is representative of the fate of a cohort as it ages through time. The assumption implies constant daily production of eggs and negligible transport of larvae into or out of the study area. Jack mackerel are serial spawners, spawning over several months. Because the experiment was conducted in the middle of the spawning season, it is not unreasonable to expect that the production of eggs was constant. We were unable to detect a change in the spatial distribution of the larvae over the 4 d sampling period. In areas where sampling was repeated, larval densities were similar. Southerly transport in May is commonly 0.2 kn in this locality (Hickey 1979); all southern stations, including those that were repeated (Stations 1 to 14), showed low larval densities (0 to 5 tow^{-1}), implying negligible transport to larvae to the south over the 4 d.

If we accept that relative abundances, measured at one time, are representative of a cohort's history through time, then larval mortality is the change in abundance. Larval growth may vary with size; thus size-specific catches must be standardized by dividing each catch by the duration of growth through the size

Table 1. *Trachurus symmetricus*. Histological condition of 4 size classes (preserved size) of field-collected jack mackerel larvae (from Theilacker in press)

	Dying	Starving	Recovering	Healthy	Total	Dying % d^{-1}
Yolk-sac	–	–	–	15	15	0
3.2 to < 3.5 mm						
Number	43	74	45	38	200	
Duration (d)	1	3	2	6		
Number d^{-1}	43	24.7	22.5	6.3	96.5	45
3.5 to < 4.0 mm						
Number	2	16	38	54	110	
Duration (d)	1	3	2	3.3		
Number d^{-1}	2	5.3	19	16.4	42.7	5
4.0 to < 4.5 mm						
Number	0	2	12	45	59	
Duration (d)	–	3	2	3.3		
Number d^{-1}	–	0.7	6	13.6	20.3	0

category. The quotients may be referred to as production rates, and when plotted against the age of each category, they define the production curve (Hewitt & Brewer 1983). The slope of the production curve measures the larval mortality rate.

Larval condition. For our estimate of starvation-induced mortality, we used the results reported by Theilacker (in press). She used a histological technique to diagnose condition of individual jack mackerel larvae (Theilacker 1978, 1981).

Special samples were taken during our study for histological analyses. These samples were preserved rapidly (in less than 8 min) to minimize tissue decomposition. Theilacker examined tissue condition of individual, ocean-caught larvae and classified each larva into a health category. Health categories corresponded to the dominant tissue condition found in larvae which were exposed to various feeding treatments in the laboratory. The number of ocean-caught larvae belonging to each health category was totaled and then adjusted for duration, which is the number of days a larva, given its state of health, is expected to remain within the size interval. For healthy larvae, the duration is simply the size interval divided by growth rate in mm d^{-1}. For example, jack mackerel belonging to the smallest size category (< 3.5 mm, Table 1) begin to eat at 3.2 mm (preserved length) and grow at .05 mm d^{-1}. The size interval for this category is 0.30 mm, and at a growth rate of 0.05 mm d^{-1}, the duration is 6 d for healthy larvae. Older larvae grow at 0.15 mm d^{-1} (see 'Larval growth'). The durations for the Dying, Starving, and Recovering categories depend on the persistence of the histological criteria used to identify these categories. In the laboratory, larvae deprived of food show the histological indicators of starving for 3 d before dying; young larvae that eat after a period of starvation show the histological criteria that identify the Recovering condition for 2 d, subsequently appearing healthy (Theilacker 1978, 1981). After the total numbers were adjusted for duration, the calculated relative proportions of larvae belonging to each health category showed that 45 % of larvae less than 3.5 mm were dying per day due to starvation. This mortality rate decreased to 5 % for 3.5 to 4.0 mm larvae, and no starvation-induced mortality was observed in jack mackerel larger than 4.0 mm (Table 1).

Larval growth. We based growth estimates on both laboratory and field data. First-feeding jack mackerel grow slowly (0.05 mm d^{-1}), and this rate of growth is difficult to discern by reading otoliths. Therefore, for first-feeding jack mackerel, we used laboratory-determined growth rates (Theilacker 1978, unpubl.), and we estimated growth of older jack mackerel by counting daily growth increments in otoliths (sagittae) of ocean-caught fish (Brothers et al. 1976).

Standard length of all larvae collected in the Bongo samples was measured and converted to 'live' size using preservative and time-in-net shrinkage correction factors (see 'Shrinkage' below). Otoliths dissected from these larvae were mounted on a slide in clear fixative (Protex) diluted with xylene. After drying for 24 h on a slide warmer, daily increments were counted under oil immersion at a magnification of 1500× using a compound light microscope. All increments from the focus to the outer edge of the otolith were included in the counts. The focus is the central area of the otolith that forms during yolk absorption and is usually void of rings. In the laboratory, jack mackerel absorb most of their yolk and begin to eat 5 d after hatching at 15 °C (Theilacker 1978). We assumed development in the field at 15.5 to 16.5 °C was the same; thus to obtain jack mackerel age, we added 5 to the number of increments. The radius of each otolith was measured to the nearest micron.

To test for differences in growth rates, larvae were grouped by sample density, high or low, and the average growth rates were compared by using an analysis of covariance. We assumed for the analysis of covariance that growth was linear (the size range of larvae collected in these samples was limited). Larvae used in the growth analysis were collected in standard Bongo hauls and preserved in alcohol. To obtain quantitative samples, Bongo nets are thoroughly hosed down before preservation. This abrasion damages larvae, causing loss of eyes and otoliths. Thus the number of larvae that could be aged was small. A total of 221 larvae were aged, 61 taken from low density samples and 160 from high density samples.

Extrusion. The length-specific catch ratio of 0.333 and 0.150 mm meshes from PAIROVET tows together with the catch ratio of 0.505 and 0.333 mm meshes from the Bongo tows was used to compute the catch ratio for

Table 2. *Trachurus symmetricus*. Size-specific sample mean and retention rates of jack mackerel larvae in 0.333 mm mesh (Column 4) and 0.505 mm mesh (Column 8) nylon nets

Preserved size (mm) (1)	PAIROVET Sample mean 0.150 mm mesh (2)	0.333 mm mesh (3)	Retention rate (4)=(3)/(2)	Bongo Sample mean 0.333 mm mesh (5)	0.505 mm mesh (6)	Retention rate (7)=(6)/(5)	Retention rate (8)=(4)×(7)
1. All tows							
2.0	0	0	–	0.10	0	–	–
2.5	0.02	0.04	2.00	1.54	0.06	0.04	0.08
3.0	0.18	0.16	0.89	2.00	0.84	0.42	0.37
3.5	0.06	0.06	1.00	0.98	1.04	1.06	1.06
4.0	0	0	–	1.76	1.68	0.95	–
4.5	0	0	–	0.72	0.72	1.00	–
5.0	0	0	–	0.98	0.90	0.92	–
5.5	0	0	–	0.26	0.32	1.23	–
6.0	0	0	–	0.06	0.14	2.33	–
6.5+	0	0	–	0.06	0.04	0.67	–
Total	0.26	0.28	1.08	8.50	5.74	0.68	
n	50	50	50	50	50	50	
2. Tows with at least 1 mesh having a positive catch							
2.0	0	0	–	0.102	0	–	–
2.5	0.05	0.10	2	1.57	0.06	0.04	0.08
3.0	0.45	0.40	0.89	2.04	0.86	0.42	0.37
3.5	0.15	0.15	1.00	1.00	1.06	1.06	1.06
4.0	0	0	–	1.80	1.71	0.95	–
4.5	0	0	–	0.73	0.73	1.00	–
5.0	0	0.05	–	1.00	0.92	0.92	–
5.5	0	0	–	0.27	0.33	1.22	–
6.0	0	0	–	0.06	0.14	2.33	–
6.5+	0	0	–	0.06	0.04	0.67	–
Total	0.65	0.70	1.08	8.63	5.85	0.68	
n	20	20	20	49	49	49	
3. Tows with both meshes having a positive catch							
2.0	0	0	–	0.12	0	–	–
2.5	0	0	–	1.76	0.07	0.04	0.03
3.0	0.75	0.50	0.67	2.36	0.98	0.42	0.28
3.5	0.50	0.50	1.00	1.00	1.17	1.06	set = 1.0
4.0	0	0	–	2.05	1.88	0.92	set = 1.0
4.5	0	0	–	0.86	0.83	0.97	set = 1.0
5.0	0	0	–	1.05	1.05	1.00	set = 1.0
5.5	0	0	–	0.24	0.38	1.58	set = 1.0
6.0	0	0	–	0.07	0.17	2.39	set = 1.0
6.5+	0	0	–	0.07	0.05	0.70	set = 1.0
Total	1.25	1.00	0.80	9.71	6.57	0.68	
n	4	4	4	42	42	42	

0.505 mm mesh compared to 0.150 mm mesh. The latter mesh was considered to be extrusion-free (Lo 1983).

From each tow, jack mackerel larvae were measured and grouped into 0.5 mm preserved length classes from 2.0 to 6.5+ mm. The sample mean catch of larvae in each length class was computed for both PAIROVET (0.150 and 0.333 mm mesh) and Bongo (0.333 and 0.505 mm mesh) for tows grouped in 3 ways: (1) all 50 tows, n = 50 for PAIROVET and Bongo respectively; (2) tows in which at least 1 net had a positive catch (number of total larvae greater than 0), n = 20 for PAIROVET and 49 for Bongo; (3) tows in which both nets had positive catches, n = 4 for PAIROVET and 42 for Bongo (Table 2). The results from Group 3 were used to estimate the length-specific retention rate of jack mackerel larvae. Although the sample size from Group 3 was extremely small for PAIROVET tows, the estimated retention rate of jack mackerel was in agreement with that of northern anchovy *Engrualis mordax*. For jack mackerel larvae, the 0.333 mm mesh retained 0.67 of the 0.150 mm mesh catch of larvae $\leq$ 3.00 mm and retained all larger larvae, whereas for anchovy larvae, the 0.333 mm mesh retained 0.63 of the 0.150 mm mesh catch of larvae $\leq$ 4.0 mm and retained all larger larvae (Lo 1983). Because few larvae of 2.0 mm length class were caught in this experiment, the catches of larvae of 2.0 mm and 2.5 mm were combined to obtain 1 retention rate for larvae $\leq$ 2.5 mm. Retention rates of jack mackerel larvae in 0.505 mm mesh compared to 0.333 mm mesh were 0.04, 0.42 and 1.00 for larvae of length classes $\leq$ 2.5, 3.0 and $>$ 3.0 mm. Products of catch ratios from PAIROVET (0.150 and 0.333 mm mesh) and Bongo (0.333 and 0.505 mm mesh) were used as estimates of retention rates of 0.505 mm mesh: 0.03, 0.28 and 1 for larvae of length classes $\leq$ 2.5, 3.0, and $>$ 3.0 mm.

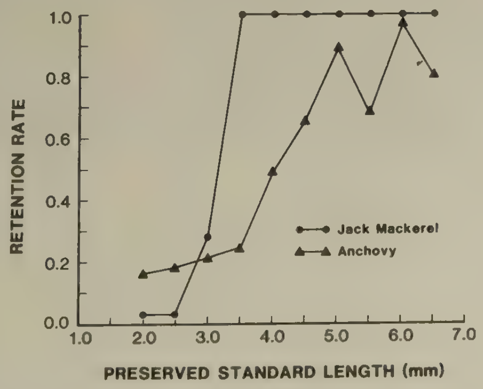

Fig. 2. *Trachurus symmetricus* and *Engrualis mordax*. Length-specific retention rates of jack mackerel and northern anchovy larvae estimated for 0.505 mm nylon mesh net

The functional relation of retention rate and length of jack mackerel was different from that of anchovy. Because there is little morphological difference between these 2 species before first feeding (< 3.0 mm), the apparent difference in retention of these larvae is probably due to the small sample size of the jack mackerel catch (Table 2; Fig. 2). The 50 % retention point is reached earlier by jack mackerel because of their greater body depth (Fig. 2).

Shrinkage. All length measurements were adjusted to be equivalent to 'live' size. Both handling and preservation cause shrinkage of larval fishes, and the amount of shrinkage is dependent on handling time (which is different for laboratory and field) and type of preservative used (Blaxter 1971, Theilacker 1980, Hay 1981). In this study, net tows for histological analyses were 5 min, and subsequent preservation in Bouin's fixative was within 3 min; Bongo tows were 20 min and subsequent net wash and preservation in formalin (fish used for size-frequency) or alcohol (fish used for aging) was within 8 min. Larval jack mackerel standard length was adjusted for shrinkage due to handling using an equation developed by Theilacker (in press):

$$y = 1.0109 - 0.0105x \qquad (1)$$

where y = the ratio of net-capture size/live size; x = net tow time.

Additional shrinkage of standard length in preservative after collection in the net was 9 % for Bouin's, 4 % for formalin, and assumed to be zero for 80 % alcohol; shrinkage of standard length for jack mackerel preserved in Bouin's in the laboratory was 8 %. Northern anchovy do not shrink in 80 % alcohol (Theilacker 1980), and we assumed that jack mackerel did not.

RESULTS

Field conditions

A temperature variation of approximately 1.5 C° was evident across the surface of the study area (Fig. 3). Zooplankton volumes and abundance of jack mackerel larvae described similar variations, more abundant at the cooler northern stations and less abundant at the warmer southern stations (Fig. 3). (Volume of zooplankton preserved in jars was checked and classified as high, low and very low.) Satellite imagery suggests that the study area may have coincided with the edge of a warm water tongue extending into cooler coastal water (Fig. 4). A temperature-salinity curve drawn from data collected within the study area agreed well with a curve obtained on an inshore station with the exception of the warm water portion of the curves (Fig. 5), suggesting a thin, warm layer of oceanic water intruding coastward over deeper coastal water. Coastal zooplankters were sampled at depths of 40 m and greater but not in the surface waters, further supporting this interpretation. Similar hydrographic features are known to persist for several weeks (P. Fiedler pers. comm.) which supports the assumption of negligible larval transport.

Growth

Larval growth rates may vary with larval condition. If larvae are competing for food in areas where the density of larvae is high, condition of some larvae may be poor, and thus average growth rates would be slower than expected. Within the sample area, a larval density gradient was apparent; densities ranged from 100 to 300 larvae per tow in the northeast quadrant to about 0 to 45 per tow in the remaining area.

The growth rate for larvae collected in areas of low larval density areas was 0.166 mm d^{-1} and for larvae collected in high density areas was 0.147 mm d^{-1}. We could not reject the null hypothesis that daily growth rates are equal ($p = 0.20$). Thus we concluded that there was no difference in growth rates of jack mackerel within the sample area, and to estimate mortality rates, we combined all samples. For larvae older than 14 d of age since fertilization, growth rates of the ocean-caught jack mackerel and laboratory-raised jack mackerel were the same (Fig. 6; Theilacker 1978, unpubl.).

Mortality

Larvae were enumerated by 0.2 mm preserved size classes; sizes were converted to live size (i.e. adjusted for shrinkage), and the results were expressed as average catch by live size category (Table 3). Catches were further adjusted for net retention and divided by the duration of growth (Fig. 7) to estimate age-specific production rates (Table 3). The duration of growth

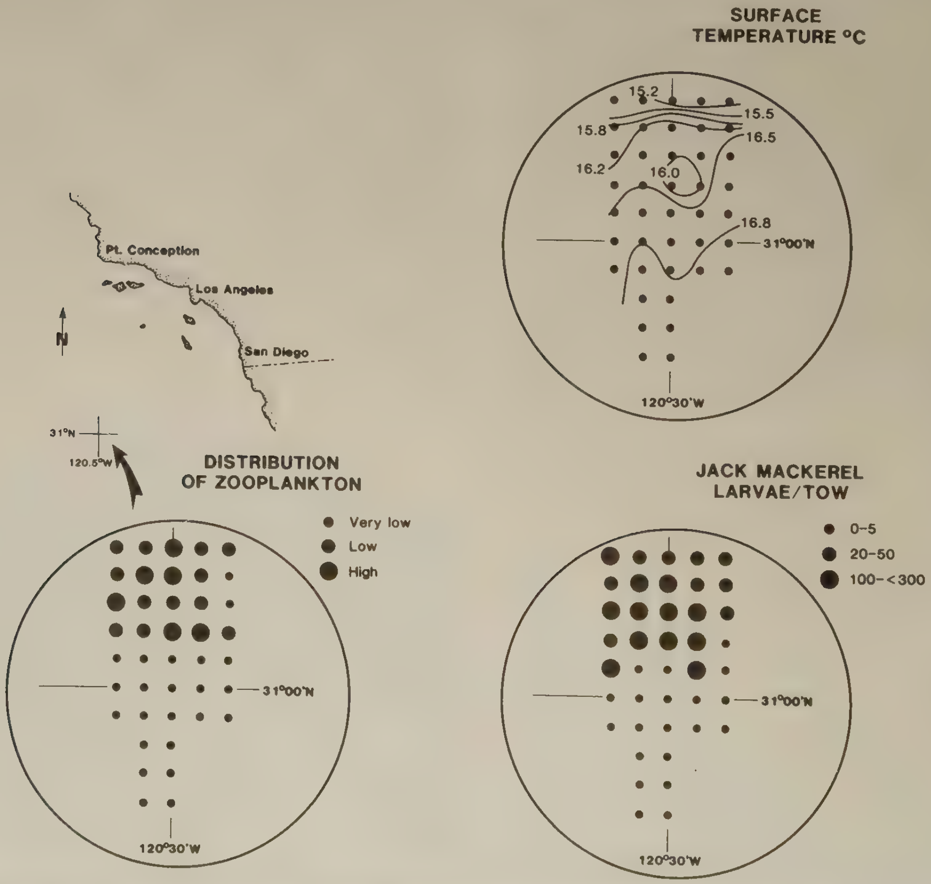
SURFACE TEMPERATURE °C
15.2
15.5
15.8
16.5
16.2
16.0
16.8
31°00'N
120°30'W
Pt. Conception
Los Angeles
San Diego
N
31°N
120.5°W
DISTRIBUTION OF ZOOPLANKTON
● Very low
● Low
● High
31°00'N
120°30'W
JACK MACKEREL LARVAE/TOW
● 0–5
● 20–50
● 100–<300
31°00'N
120°30'W

Fig 3. Temperature, zooplankton and jack mackerel distributions over the study area. All showed north-to-south gradients

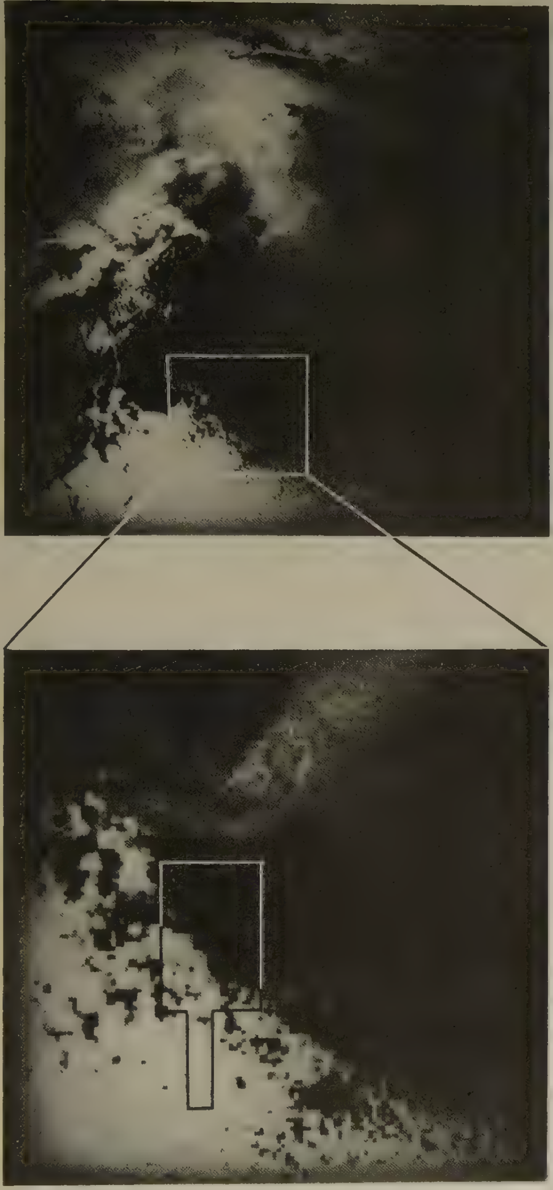

Fig. 4. NOAA 6 weather satellite imagery of sea surface temperature obtained during study period (P. Fiedler); light shading indicates warm water and dark shading indicates cool water. Upper image: prevailing surface thermal structure over the Southern California Bight; lower image: enlargement of study area with station grid outlined

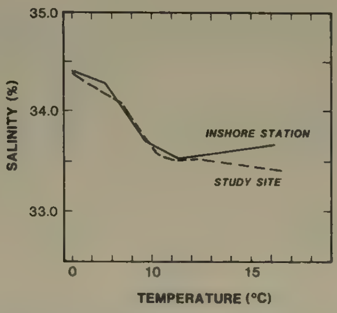

Fig. 5. Temperature/salinity curves drawn from profiles obtained from the study area and from 30 km off the coast

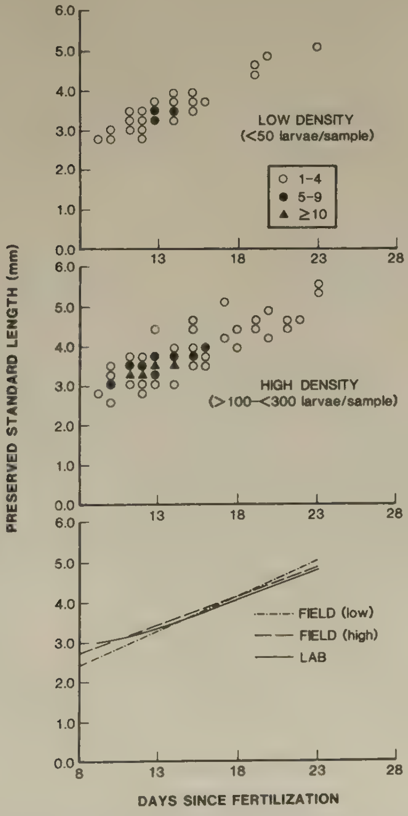

Fig. 6. *Trachurus symmetricus*. Growth of jack mackerel at low and high density stations compared to growth observed in the laboratory. Symbols in the insert show number of larvae examined

through the size categories was estimated directly from the growth curve (Fig. 7). The plot of production rate on age defines the production curve (Fig. 8) as very steep through the yolk-sac stage with survival rapidly improving as the larvae develop. Instantaneous daily mortality rate Z(t) was modeled as continuously declining with age using a Pareto-type function, $Z(t) = 1/P_t(dP_t/dt) = -\beta/t$ (Hewitt & Brewer 1983), where P_t = production at age t, measured from the moment of fertilization; β = larval mortality coefficient (Fig. 9).

Table 3. *Trachurus symmetricus.* Size-specific average catch and production rates of jack mackerel larvae. Duration of growth estimated from Fig. 7

Preserved size (mm)	Live size (mm)	Age since fertilization (d)	Retention rate	Duration of growth (d)	Catch[a] (larvae tow^{-1})	Production rate (larvae [tow d]$^{-1}$)
2.6	3.30	4.25	0.03	1.0	5.27	175.67
2.8	3.56	6.67	0.28	3.25	12.36	13.57
3.1[b]	3.94	11.63	0.28	7.25	26.86	13.25
3.4	4.32	16.37	1.00	2.25	7.32	3.25
3.6	4.57	18.63	1.00	2.25	4.55	2.02
3.8	4.83	20.87	1.00	2.25	1.64	0.73
4.0	5.08	23.12	1.00	2.25	0.68	0.30

[a] Larvae tow^{-1} = larvae (unit m^3)$^{-1}$ (m depth)$^{-1}$

[b] Size Groups 3.0 and 3.2 mm combined due to insufficient data

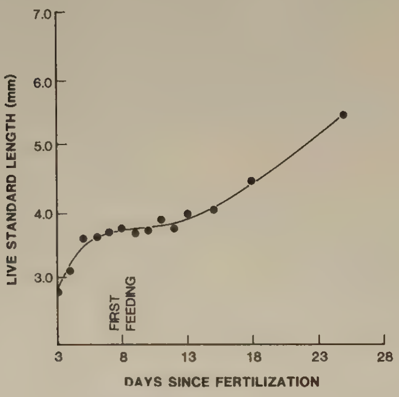

Fig. 7. *Trachurus symmetricus.* Growth of jack mackerel larvae as observed in the laboratory (Theilacker 1978, unpubl.) Curve fitted by eye

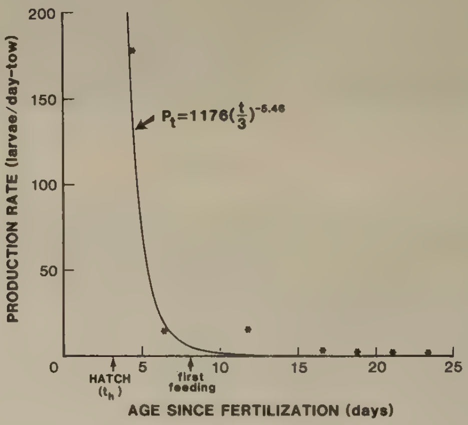

Fig. 8. *Trachurus symmetricus.* Production curve of jack mackerel larvae. Data from Table 3

By integrating Z(t) from the time of hatch (t_h), the production curve may be expressed as:

$$P_t = P_h (t/t_h)^{-\beta} \text{ for } t > t_h \qquad (2)$$

For t_h = 3 d, P_h = 1176 and β = 5.46.

After linearization by logarithmic transformation on both sides of the equation, the Pareto-type mortality curve fitted to jack mackerel data yields r^2 = 0.88. This high r^2 indicates that the Pareto-type mortality curve is an appropriate model to describe the mortality process of jack mackerel. Total instantaneous daily mortality rate and daily starvation mortality rates (percent dying per day) are compared in Fig. 9. The total mortality rate is the sum of starvation and predation mortality rates. In this study, the total mortality rate and the starvation mortality rate were estimated by 2 different procedures. Due to small sample size and the difference in estimation procedures, it is possible to observe an estimated starvation rate greater than the total mortality as shown for the larvae of 11 to 12 d old in Fig. 9. In

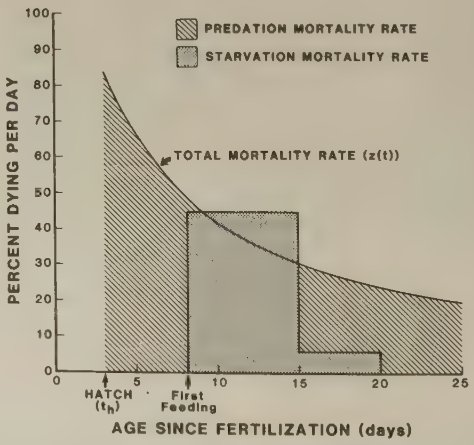

Fig. 9. *Trachurus symmetricus.* Total mortality rate of larval jack mackerel as a function of age since fertilization. Mortality due to predation + mortality due to starvation = total mortality (see text)

this case, one could conclude that the starvation constitutes the major portion of the total mortality. For yolk-sac larvae (prior to first feeding), starvation is not a source of mortality and the large losses (50 to 80 % d^{-1}) are due to predation. As larvae absorb yolk and begin to search for food, starvation becomes a significant source of mortality with losses at this life stage being about 45 % d^{-1}. As larvae develop further, their ability to capture food rapidly improves and predation again becomes the major source of mortality, although at a much reduced rate (20 % d^{-1}).

DISCUSSION

By comparing starvation mortality with total mortality, we have shown that starvation was a significant cause of death for first-feeding larval jack mackerel in a relatively oligotrophic portion of the spawning habitat. Theilacker (in press) estimates approximately 4-fold reduction in starvation rate of first-feeding larvae near islands and banks, where food is more abundant. However, we have no estimate of total mortality for jack mackerel larvae in the nearshore zone. It is unreasonable to expect starvation to account for all of the mortality at the time of first feeding (as indicated in Fig. 9). Because of the small sample size, there may be considerable errors associated with the estimates of total and starvation mortality. We are, however, confident about the qualitative content of our conclusions.

In terms of numbers removed, predation appeared to be the most important source of mortality. Predation was most severe during the yolk-sac phase. From the production curve (Fig. 8), we estimate that 99 % of hatching larvae were removed prior to yolk-absorption. Predation may be even more harsh during the early embryonic period prior to hatching. Estimated losses from fertilization to yolk-sac absorption range from 99.5 % to 99.9 %. Predation was the dominant source of mortality, but at a much reduced rate, once larvae had successfully fed and developed motility. Dramatic reduction in the vulnerability of actively feeding larval anchovy to predation has been reported by Lillelund & Lasker (1971), Theilacker & Lasker (1974) and Webb (1981). Hunter (1981, 1984) lists crustacea, chaetognaths, medusea, ctenophores and planktivorous fish as known predators of fish eggs and larvae. But sibling cannibalism may be the main source of mortality on clusters of eggs and yolk-sac larvae; Grave (1981) estimates that Atlantic mackerel *Scomber scombrus* larvae constitute 83 % of the diet of larger mackerel larvae.

The size-specific larval production (P_t) used in modelling the mortality curve was corrected by an extrusion factor (Table 3). The extrusion study indicated that 0.505 mm mesh net retained 3 % of larvae < 2.5 mm. If in fact the true retention is greater than 3 %, the mortality for yolk-sac larvae, which is due to predation, would be overestimated. However, subsequent partitioning of total mortality into starvation and predation would remain the same.

In our computation of total mortality rate, we assumed a steady state, i.e. that daily egg production was constant and that each cohort experienced the same daily mortality rate. Even though jack mackerel are serial spawners, egg production may vary due to adults moving into and out of the area, and age-specific daily mortalities may vary between cohorts. We realize that our data are insufficient to test these assumptions. However, we believe our approach of partitioning the total mortality of young fish into starvation and predation provides useful information for future studies. Despite sparse data, our results give a good indication of when each of the 2 causes of mortality dominate during the life stage. Future studies are recommended to verify our results and to test the assumptions that we made.

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LITERATURE CITED

Blaxter, J. H. S. (1971). Feeding and condition of Clyde herring larvae. Rapp. P-v. Réun. Cons. int. Explor. Mer 160: 128–136

Brothers, E. B., Mathews, C. P., Lasker, R. (1976). Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. U. S. 74 (1): 1–8

Ellertsen, B., Mokness, E., Solemdal, P., Tilseth, S., Westgard, T., Oiestad, V. (1981). Growth and survival of cod larvae in an enclosure. Experiments and a mathematical model. Rapp. P.-v Réun Cons. int. Explor. Mer 178: 45–57

Grave, H. (1981). Food and feeding of mackerel larvae and early juveniles in the North Sea. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 454–459

Hay, D. E. (1981). Effects of capture and fixation on gut contents and body size of Pacific herring larvae. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 395–400

Hewitt, R. P. (1981). The value of pattern in the distribution of young fish. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 229–236

Hewitt, R. P and Brever, G. D. (1983). Nearshore production of young anchovy. Calif. Coop. Ocean. Fish. Invest. (CalCOFI) Rep XXIV: 235–245

Hickey, B. M. (1979). The California Current System – hypotheses and facts. Prog. Oceanogr. 8: 191–279

Hunter, J. R. (1981). Feeding ecology and predation of marine fish larvae. In: Lasker, R. (ed.) Marine fish larvae: morphology, ecology and relation to fisheries. Wash. Sea Grant, Univ. Wash. Press, Seattle, p. 33–77

Hunter, J. R. (1984). Inferences regarding predation on the early life stages of cod and other fishes. Flodevigen rapportser. 1, The propagation of cod, *Gadus morhua* L.: 533–562

Lillelund, K., Lasker, R. (1971). Laboratory studies on predation by marine copepods on fish larvae. Fish. Bull. U. S. 69: 655–667

Lo, N. C. H. (1983). Re-estimation of three parameters associated with anchovy egg and larval abundance: temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. National Oceanic and Atmospheric Administration, La Jolla, NOAA-TM-NMFS-SWFC-31: 1–33

Methot, R. D. Jr., Kramer, D. (1979). Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull. U. S. 77: 413–423

O'Connell, C. P. (1980). Percent of starving northern anchovy larvae *(Engraulis mordax)* in the sea as estimated by histological methods. Fish. Bull. U. S. 78: 475–489

Shepherd, J. G., Cushing, D. H. (1980). A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. Cons. int. Explor. Mer 39: 160–67

Smith, P. E., Richardson, S. (1977). Standard techniques for pelagic fish egg and larva surveys. FAO, Fish. Tech. Pap. 175: 100

Theilacker, G. H. (1978). Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus,* larvae. Fish. Bull. U. S. 76: 403–414

Theilacker, G. H. (1980). Changes in body measurements of larval northern anchovy, *Engrualis mordax,* and other fishes due to handling and preservation. Fish. Bull. U. S. 78: 685–692

Theilacker, G. H. (1981). Effect of feeding history and egg size on the morphology of jack mackerel, *Trachurus symmetricus,* larvae. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 432–440

Theilacker, G. H. (in press.) Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus,* determined with histological and morphological methods. Fish. Bull. U. S. 84

Theilacker, G. H., Lasker, R. (1974). Laboratory studies of predation by euphausid shrimps on fish larvae. In: Blaxter, J. H. S., (ed.) The early life history of fish. Springer-Verlag, Berlin, p. 287–299

Webb, P. W. (1981). Responses of northern anchovy, *Engraulis mordax,* larvae to predation by a biting planktivore, *Amphiprion percula.* Fish. Bull. U. S. 79: 727–735

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Comparison of Constant Effort Harvest Policies for Fish Stocks with Variable Recruitment

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Environmental variability may have a substantial influence on marine fish stocks, primarily by affecting survival to the time of recruitment. Simulation studies at low, intermediate, and high levels of variability in recruitment were used to compare alternative constant effort policies for anchovy (*Engraulis capensis*), Atlantic menhaden (*Brevoortia tyrannus*), and Pacific ocean perch (*Sebastes alutus*) fisheries. These policies were either to maintain effort at the level producing maximum sustainable yield (f_{MSY}), or to permit levels of effort 25–100% greater than f_{MSY}. An increase in effort of 25% above f_{MSY} typically did not reduce annual yield significantly; however, a significant reduction in yield was apparent in all cases when effort increased by 75–100%. When recruitment is highly variable, comparable yields may be obtained at several levels of fishing effort. In such cases, environmental variability provides the fishery manager with considerable flexibility to enhance social or economic benefits without decreasing yields significantly.

La variabilité environnementale peut avoir une influence importante sur les stocks de poissons marins, surtout pour la survie jusqu'à l'époque du recrutement. On a utilisé des études de simulation à des niveaux de variabilité du recrutement faible, intermédiaire et élevé pour comparer divers régimes d'effort constant pour la pêche de l'anchois (*Engraulis capensis*), de l'alose tyran (*Brevoortia tyrannus*) et du sébaste à longue mâchoire (*Sebastes alutus*). Ces régimes visaient soit le maintien de l'effort au niveau produisant un rendement maximal soutenu (f_{RMS}) ou un accroissement des niveaux d'effort le rendant de 25 à 100 % plus élevé que le f_{RMS}. Un effort supérieur de 25 % au f_{RMS} n'a pas abaissé le rendement annuel de façon significative ; toutefois, une baisse importante du rendement était évidente dans tous les cas quand l'effort était supérieur de 75 à 100 %. Quand le recrutement est très variable, on peut obtenir des rendements comparables à plusieurs niveaux d'effort de pêche. Dans de tels cas, la variabilité environnementale procure une grande latitude au gestionnaire des pêches pour accroître les avantages sociaux ou économiques sans abaisser nettement les rendements.

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Management plans for the regulation of commercial fisheries usually restrict either fishing effort or catch. Catch quotas have received greater use historically (Sissenwine and Kirkley 1982); however, imposi- on of a catch quota may lead to stock depletion after several ears of poor recruitment (Swartzman et al. 1983). In addition, esired fishing mortality rates are achieved more directly by gulation of fishing effort than by catch restrictions (Sissen- ine and Kirkley 1982). For these reasons, this study is based n a comparison of management plans in which harvests are gulated through restrictions on fishing effort.

Development of an effective management plan is difficult ecause environmental factors may have a substantial influence n fish stocks, primarily by affecting survival to the time of cruitment (Getz and Swartzman 1981). A direct effect of this riability in year-class strength is variability in annual catch ulland 1972, 1982; Hennemuth et al. 1980), and a fishery ay be supported for several years largely by a single strong year-class. An indirect effect of this phenomenon is that, because stock size is not constant, the optimal level of fishing effort also varies. This suggests that similar harvests may be obtained at a range of effort levels; therefore, moderate errors in estimating the optimal level of fishing effort would be acceptable. In addition, flexibility in selecting effort regulations might enable the fishery manager to enhance social or economic benefits without decreasing yields significantly.

Simulation studies have been useful in evaluating alternative fishery management plans. For example, Huang and Walters (1983) compared alternative strategies for rehabilitation of a large yellow croaker (*Pseudosciaena crocea*) stock and Archibald et al. (1983) estimated steady-state yields obtained from a Pacific ocean perch (*Sebastes alutus*) stock at different levels of fishing effort. In both studies, variability in recruitment was simulated by incorporating an error term into the stock–recruitment relationship (SRR). Simulation studies might also be used to compare frequency distributions of annual harvest obtained at different levels of fishing effort. This comparison may be informative because, even though steady-state or expected yield differs at different levels of fishing effort, such differences may not be of practical importance.

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Consider, for example, regulation of a fishery in which the stock is moderately overexploited and alternative employment is not available. In this case, expected yield will be increased by imposition of a theoretically optimal management plan (optimal in the sense that yield is maximized). The management plan also may have substantial socioeconomic impacts because maximum sustainable yield (MSY) is obtained by decreasing fishing effort, and these impacts could be unacceptable if observed yields did not increase noticably. The success of any MSY policy depends not only on the accuracy of supporting biological data and compliance within the fishery, but also on the unpredictable effect of the environment on recruitment. By incorporating an appropriate error term into the SRR, age-structured models can be used to predict whether observed changes in yield brought about by decreasing effort will be worth the accompanying socioeconomic disruption.

In this study, we examined published data on stock size and recruitment to determine typical levels of variability in recruitment. Simulation studies at low, intermediate, and high levels of variability were used to compare alternative management policies for anchovy (*Engraulis capensis*), Atlantic menhaden (*Brevoortia tyrannus*), and Pacific ocean perch fisheries. Using maximization of yield as a management goal, these comparisons were done to predict changes in yield that result from changes in fishing effort for fish of varying life spans at three levels of environmental variability.

Methods

The Stock–Recruitment Relationship

Several models of varying complexity have been proposed to examine the relationship between parental stock and recruitment (Beverton and Holt 1957; Cushing 1971; Larkin 1973; Ricker 1975; Getz and Swartzman 1981; Shepherd 1982). Minimum features required for a biologically realistic SRR are (1) low recruitment at very low stock sizes and (2) the ability to allow recruitment to vary widely at intermediate stock sizes (Shepherd 1982; Swartzman et al. 1983; Strong 1984). The Ricker and Beverton–Holt stock–recruitment models are most commonly used to model fish populations, and both models predict lower recruitment as stock size approaches zero. To introduce an appropriate level of environmental variability into the SRR, it is first necessary to determine what form this term should take.

A multiplicative lognormal error term has been used in recent studies of stock–recruitment models (Allen 1973; Walters and Hilborn 1976; Peterman et al. 1978; Laurec et al. 1980; Peterman 1981; Walters and Ludwig 1981; Archibald et al. 1983; Huang and Walters 1983) of the general form

$$R = f(S)e^{\upsilon}$$

where R = recruitment, $f(S)$ = some function of parental stock, which is often represented by biomass of spawners (Beverton 1962; Doubleday 1976; Deriso 1980; Shepherd 1982), and υ = normally distributed random variate with mean 0 and variance σ^2.

This multiplicative lognormal error term has been used in studies of salmon populations, both for mathematical convenience as well as for assumed biological realism (Peterman 1981). A theoretical justification for use of this error term is that e^{υ} can be viewed as a random survival factor resulting from several independent and multiplicative environmental factors (Walters and Hilborn 1976). Thus, υ represents the sum of several random factors and should be approximately normally distributed by the Central Limit Theorem (Walters and Hilborn 1976). The lognormal error distribution is biologically appealing because it provides a simple representation of the observed effects of environmental variability (i.e. good environmental conditions can produce very large year-classes, while poor environmental conditions can reduce recruitment to zero at most). In addition, increased variability in recruitment would seem more likely when the spawning stock is large (Gulland 1967), and use of a multiplicative error term assumes that variability will increase as stock size increases. The lognormal distribution also more accurately represents the frequency distribution of observed year-class strength (Hennemuth et al. 1980) and salmonid survival rates (Peterman 1981) than the normal distribution.

In this paper, we assume that a lognormal error term is appropriate and estimate the magnitude of the lognormal error variance for 13 multi-aged marine fish stocks (Table 1). Minimum criteria for inclusion of a data set were as follows: (1) at least 10 yr of data were available, (2) parental stock was estimated either as stock biomass, biomass of spawners, or a measure of egg production, and (3) recruitment was given as numbers of fish.

Three models were fitted to each data set for the following reasons. For a particular stock, model selection may be based on biological information (Nelson et al. 1977); however, alternative models can rarely be excluded using statistical tests (Gulland 1967). Second, because a regression estimate of the residual error variance includes both the true random error and a lack-of-fit component, we used three possible models to evaluate the sensitivity of our estimates to the form of the model:

(1) $R = \mu e^{\upsilon}$

(2) $R = \alpha S e^{-\beta S} e^{\upsilon}$

(3) $R = 1/(\gamma + \delta/S)e^{\upsilon}$

where μ, α, β, γ, and δ are parameters. The first model assumes that no relationship exists between stock size (S) and recruitment (R). The second is the Ricker model (Ricker 1975) and the third is that of Beverton and Holt (Ricker 1975). A constant recruitment model was included to evaluate the increase in error variance which results from the use of a simpler (and conceptually different) model, although the model violates the above criterion that recruitment should decrease at very low stock sizes.

Because the log-transformed Ricker model is a linear equation and has an additive error term, the residual error variance (σ^2) was estimated using linear regression. The Beverton–Holt model was fitted with nonlinear regression as $\ln(R) = \ln(1/(\gamma + \delta/S)) + \upsilon$ to obtain an estimate of σ^2. Initial parameter estimates for the Beverton–Holt model were obtained by transforming the model to use linear least-squares regression (Ricker 1975), and these estimates were used as starting values for nonlinear regression analysis. Bounded nonlinear regression (SAS Institute, Inc. 1982) was required to obtain reasonable parameter estimates ($\delta > 0$) for one stock, the North Sea plaice; Ricker (1975) also noted this problem when fitting a Beverton–Holt curve to these data using linear regression.

Parameterization of Age-Structured Model

To explore the relationship between number of age classes (λ) and response to overexploitation, parameter estimates were

TABLE 1. Description of the 13 fish stocks used to estimate the level of random variability in the stock–recruitment relationship. The number of observations in each data set is given as N.

Common name	Scientific name	Area	N	Source[a]
Herring	*Clupea harengus*	Norwegian[b]	20	A
		Georges Bank	13	B
		Icelandic[b]	23	C
		Icelandic[c]	29	C
Round herring	*Etrumeus teres*	South Africa	13	D
Sardine	*Sardinops caerulea*	California	33	E
Atlantic menhaden	*Brevoortia tyrannus*	Atlantic	16	F
Pacific halibut	*Hippoglossus stenolepis*	Pacific	46	G
Plaice	*Pleuronectes platessa*	North Sea	26	H
Pilchard	*Sardinops ocellata*	South Africa	26	D
Anchovy	*Engraulis capensis*	South Africa	13	D
Atlantic mackerel	*Scomber scombrus*	Northwest Atlantic	16	I
Large yellow croaker	*Pseudosciaena crocea*	China Sea	22	J

[a] Source: A, Dragesund et al. 1980; B, Anthony and Waring 1980; C, Jakobsson 1980; D, Newman and Crawford 1980; E, Troadec et al. 1980; F, Nelson et al. 1977; G, Deriso and Quinn 1983; H, Ricker 1975; I, Anderson and Paciorkowski 1980; J, Huang and Walters 1983.

[b] Spring-spawning.

[c] Summer-spawning.

TABLE 2. Parameter estimates for the age-structured model of anchovy stock dynamics (from Getz 1985). Number of age-classes (excluding age 0): $\lambda = 5$; length of harvesting season: $t' = 0.67$ yr; stock–recruitment model: Beverton–Holt (spawning after harvesting season), parameter estimates: $\hat{\gamma} = 0.0082$, $\hat{\delta} = 0.9016$; lognormal error variance: $s^2 = 0.06$[a]; range of effort levels (arbitrary multipliers) used in simulations: $f = 0$–4.

Age	Weight (g)	Fecundity index (g)[b]	Catchability (normalized)	Natural mortality
1	1.6	0.8	0.24	0.8
2	6.9	6.9	0.36	0.8
3	14.0	14.0	0.42	0.8
4	19.0	19.0	1.00	0.8
5	24.0	24.0	1.00	0.8

[a] An estimate of the lognormal error variance was obtained from total stock biomass and recruitment estimates from 1964 to 1976 (Newman and Crawford 1980). Getz (1980) obtained parameter estimates for the Beverton–Holt SRR using estimates of spawning stock biomass and recruitment from 1964 to 1978 but did not publish the stock–recruitment data.

[b] Average weight multiplied by the proportion that are fecund.

obtained for a relatively short-lived anchovy stock ($\lambda = 5$) from the west coast of South Africa (Table 2; from Getz 1985) and for a relatively long-lived stock of Pacific ocean perch ($\lambda = 29$) (Table 3; from Archibald et al. 1983). Note that λ represents the maximum age-class used in the model, and not the life span of the fish. Recent aging studies using sectioned otoliths indicate that Pacific ocean perch may live for more than 70 yr (Archibald et al. 1981). Data used in this simulation study were obtained through stock reconstruction (Archibald et al. 1983), using catch-at-age data obtained by surface readings of otoliths. Sufficient data are not yet available from aging otolith sections to permit reanalysis. Parameter estimates for Atlantic menhaden, a fish of intermediate life span ($\lambda = 8$), were obtained primarily from life history studies and previous analyses of catch and effort data (Table 4). (In-depth analyses of the Atlantic menhaden fishery are given by Schaaf and Huntsman (1972), Schaaf (1975), Nelson et al. (1977), and Schaaf (1979).) Numbers-at-age were obtained from cohort analysis (Pope 1972) using catch-at-age and fishing effort data (Schaaf 1979) and estimates of mean instantaneous natural mortality rate ($M = 0.25$) and mean catchability (Vaughan 1977). As in earlier studies of Atlantic menhaden stock dynamics (Schaaf and Huntsman 1972; Nelson et al. 1977; Schaaf 1979), the Ricker curve was used to represent the SRR. Spawning potential was represented by the estimated biomass of spawning females, and was obtained as

$$\sum_{i=1}^{\lambda} c_i N_{it}$$

where N_{it} is the number of age-i fish in year t and c_i, the fecundity parameter for age-i fish, is defined as

$$c_i = s_i f_i w_i$$

where s_i = proportion of females that are sexually mature at age i (Vaughan 1977), f_i = proportion of age i fish that are females (Reintjes 1969), and w_i = weight of females at age i + 0.5 from a von Bertalanffy growth curve (Reintjes 1969).

Estimates of weight-at-age were obtained by using sex-specific von Bertalanffy curves (Reintjes 1969) to predict mean weight at ages 1.5–8.5. A von Bertalanffy curve was fitted to data for both sexes and used to predict overall mean weight-at-age.

Evaluation of Alternative Constant Effort Policies

Once typical levels of variability in recruitment were determined, it was possible to evaluate the effects of this variability on alternative constant effort policies. This was done by incorporating a lognormal error term into an age-structured model containing a SRR; a complete description of such a model is given by Archibald et al. (1983) or Huang and Walters (1983).

To estimate MSY for each stock, estimates of steady-state average yield were obtained at each level of fishing mortality using the following replication–deletion approach (Law and Kelton 1982). Each of 100 replicates was run for 10λ yr, and average annual yield was obtained for the last 5λ yr. Observations from the first 5λ yr were deleted to reduce the influence of the nominal set of initial conditions.

TABLE 3. Parameter estimates for the age-structured model of Pacific ocean perch stock dynamics (from Archibald et al. 1983). Recruitment occurs at age 6, so weight, catchability, and natural mortality are set to 0 for ages 1–5. Number of age-classes (excluding age 0): $\lambda = 29$; length of harvesting season: $t' = 1.00$ yr; stock–recruitment model: Ricker (spawning at start of year), parameter estimates: $\hat{\alpha} = 0.0883$, $\hat{\beta} = 9.01 \times 10^{-5}$; lognormal error variance: $s^2 = 0.30$; range of effort levels (arbitrary multipliers) used in simulations: $f = 0.0$–0.40.

Age	Weight (10^{-2} kg)	Fecundity index	Fishing mortality[a]	Natural mortality
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	0
5	0	0	0	0
6	0.00485	0	0.010	0.05
7	0.00529	0	0.021	0.05
8	0.00572	0	0.040	0.05
9	0.00614	0	0.069	0.05
10	0.00654	0	0.111	0.05
11	0.00694	1.00	0.162	0.05
12	0.00732	1.22	0.217	0.05
13	0.00770	1.47	0.266	0.05
14	0.00806	1.72	0.297	0.05
15	0.00841	1.97	0.304	0.05
16	0.00876	2.20	0.284	0.05
17	0.00909	2.44	0.243	0.05
18	0.00942	2.67	0.190	0.05
19	0.00973	2.92	0.190	0.05
20	0.01000	3.11	0.190	0.05
21	0.01030	3.31	0.190	0.05
22	0.01060	3.48	0.190	0.05
23	0.01090	3.65	0.190	0.05
24	0.01120	3.83	0.190	0.05
25	0.01150	3.83	0.190	0.05
26	0.01170	3.83	0.190	0.05
27	0.01200	3.83	0.190	0.05
28	0.01220	3.83	0.190	0.05
29+	0.01300	3.83	0.190	0.05

[a] B. M. Leaman, Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C., pers. comm. These estimates of fishing mortality at age in 1977 were obtained through stock reconstruction (Archibald et al. 1983) and were multiplied by arbitrary constants (termed effort) to produce desired levels of fishing mortality.

TABLE 4. Parameter estimates for the age-structured model of Atlantic menhaden stock dynamics. Number of age-classes (excluding age 0): $\lambda = 8$; length of harvesting season: $t' = 1.00$ yr; stock–recruitment model: Ricker (spawning at start of year), parameter estimates: $\hat{\alpha} = 0.0205$, $\hat{\beta} = 0.0024$; lognormal error variance: $s^2 = 0.25$; range of effort levels (vessel-weeks) used in simulations: $f = 0$–1000.[a]

Age	Weight (g)	Fecundity index (g)	Catchability[b]	Natural mortality
1	102.77	0	0.000577	0.25
2	260.21	110.25	0.001805	0.25
3	411.73	227.37	0.001579	0.25
4	530.31	302.70	0.001540	0.25
5	614.28	354.63	0.001430	0.25
6	670.60	410.44	0.001820	0.25
7	707.23	491.98	0.001703	0.25
8	730.63	496.60	0.001703	0.25

[a] Estimates of annual effective fishing effort (adjusted for changes in catchability using 1971 as the base year) are given by Schaaf (1979). The range 0–1000 vessel-weeks includes most observed values and all published estimates of the level of fishing effort that produces MSY.

[b] Age-specific catchability estimates were obtained from cohort analysis. Effective fishing effort data (Schaaf 1979) and an estimate of mean catchability (Vaughan 1977) were used to obtain starting values for fishing mortality rates.

Once MSY and the associated level of fishing effort (f_{MSY}) were estimated, simulation studies were used to compare the MSY effort policy with constant effort policies where effort was 25, 50, 75, and 100% greater than f_{MSY}. Each treatment combination represented one of three levels of variability in recruitment, one of three fish stocks, and one of four pairwise comparisons of f_{MSY} versus an alternative effort level. The starting age distribution for each simulated period of $k = 5\lambda$ yr was obtained from a deterministic version of the model (Getz 1980), using the level of effort that produced MSY for the deterministic model.

Because the commercial fisherman is affected by annual changes in recruitment and subsequent fluctuations in harvest, we emphasized annual harvest rather than mean or total harvest. However, consecutive harvests in each k-yr period are not independent, and harvests in the first few years are affected by the starting conditions. To obtain independent replicates that are less biased by initial conditions and therefore better estimates of steady-state responses, we analyzed only the harvest from year k in each k-yr period. Harvests in years 1 through $k - 1$ also would be of interest to the fisherman and fishery manager. However, these harvests would tend to be more similar among treatments than harvests in year k due to the shared starting conditions. By focusing the analysis on the steady-state behavior of the system, we obtain conservative results about the similarity in performance of alternative policies. One hundred replicates were used for each treatment. Note that the sample size is arbitrary and that our ability to detect differences among treatments would increase with an increase in sample size. We contend that a difference of practical significance should be detectable by observing 100 independent trials, and note that only a single trial would be observed after implementation of a management plan. Differences in the frequency distribution of harvest in year k were tested at the 95% confidence level using a two-tailed Kolmogorov–Smirnov test (Siegel 1956).

Results and Discussion

Few of these stocks displayed evidence of a relationship between stock size and recruitment, and neither the Ricker nor Beverton–Holt curve appeared to account for a significant amount of variation in recruitment. Estimates of σ^2 (s^2) ranged from 0.06 to 1.20 for both the Ricker and Beverton–Holt models. Under the assumption that no relationship exists between stock size and recruitment, s^2 ranged from 0.07 to 5.68. The distribution of s^2 was similar for the three models (Fig. 1), and in all but two cases (California sardine and Icelandic spring-spawning herring), s^2 does not increase substantially when no relationship between stock size and recruitment is assumed. For the three models considered, most values were less than 0.75, and three values were selected arbitrarily to represent low (0.25), moderate (0.50), and high (0.75) levels of

TABLE 5. Comparison of annual yields obtained at the level of fishing effort that produced maximum sustainable yield (f_{MSY}) with yields obtained when effort exceeded f_{MSY} by 25, 50, 75, or 100%. For each paired comparison, frequency distributions of annual yield were compared using a Kolmogorov–Smirnov test ($\alpha = 0.05$), and significant differences are denoted by the letter *Y*. Estimates of the percentage increase in variability in steady-state average yield are given in parentheses as $100 \times (CV_i - CV_{MSY})/CV_{MSY}$, where CV_{MSY} and CV_i represent coefficients of variation when effort equals f_{MSY} or exceeds f_{MSY} by i = 25, 50, 75, or 100%. Three values of the lognormal error variance (σ^2) were used to represent levels of environmental variability in the period following implementation of a management plan.

	Increase in effort above f_{MSY} (%)											
	$\sigma^2 = 0.25$				$\sigma^2 = 0.50$				$\sigma^2 = 0.75$			
	25	50	75	100	25	50	75	100	25	50	75	100
Anchovy	*N* (−13)	*N* (24)	*Y* (45)	*Y* (72)	*N* (24)	*N* (23)	*Y* (48)	*Y* (50)	*N* (0)	*N* (38)	*Y* (31)	*Y* (44)
Menhaden	*N* (10)	*Y* (45)	*Y* (109)	*Y* (118)	*N* (27)	*Y* (60)	*Y* (43)	*Y* (106)	*N* (22)	*N* (13)	*Y* (60)	*Y* (113)
Perch	*Y* (57)	*Y* (13)	*Y* (114)	*Y* (138)	*N* (18)	*N* (36)	*Y* (64)	*Y* (120)	*N* (15)	*N* (31)	*Y* (90)	*Y* (164)

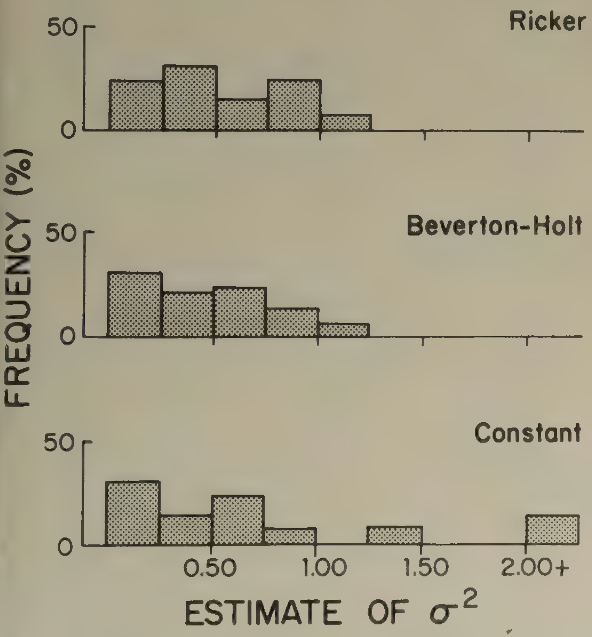

FIG. 1. Sample distribution of s^2, the error variance of the stock–recruitment relationship, for 13 multi-aged fish stocks. Ricker, Beverton–Holt, and constant recruitment models were fitted to each data set and a multiplicative lognormal error term was assumed.

variability for a general evaluation of the effect of variability in recruitment on alternative management scenarios.

For the simulated anchovy fishery, changes in the level of environmental variability had no detectable impact on comparisons of alternative policies (Table 5). For the Atlantic menhaden and Pacific ocean perch fisheries, increases in environmental variability obscured differences in yield obtained at different levels of fishing effort.

An increase in effort of 25% above f_{MSY} typically did not decrease yield significantly (Fig. 2; Table 5). Significantly lower yields were obtained in all cases when effort increased by 75–100% above f_{MSY}. It should be noted that the Kolmogorov–Smirnov test is sensitive to differences in location or dispersion (Siegel 1956); hence, significant differences may be due in part to increased variability in yield associated with increased fishing effort (Table 5). These results suggest that, even if future levels of environmental variability are relatively high, reductions in effort for heavily fished stocks should provide higher and less variable annual yields. When differences between current effort and f_{MSY} are less than 25–50% of f_{MSY}, changes in the magnitude or variability of annual yield may be insufficient to justify implementation of an MSY policy.

The approach demonstrated here can be used to contrast the effectiveness of any alternative policies that require different levels of fishing effort. Alternative policies might arise from different management models, from using different parameter estimates for a single model, or from a comparison of theoretically optimal and current levels of effort. The theoretically optimal or target level of effort need not be f_{MSY}. For example, Doubleday (1976) noted that when effort is reduced below f_{MSY}, losses in average yield may be offset by increases in catch per unit effort or reductions in the variability of yield. Selection of a target level of effort or index of policy performance is dependent on the fishery manager's objectives. In this study, yield maximization was assumed to be the management objective, and we evaluated changes in the distribution of annual harvest. However, changes in the distribution of catch per unit effort or net income may be equally important outcomes of a change in the level of fishing effort. Finally, stochastic models also can be used for risk analysis; for example, they can be used to estimate the probability that stock biomass will fall below an arbitrary level (Getz and Swartzman 1981; Archibald et al. 1983).

Further evidence that yield may be comparable at several levels of fishing effort was provided by Getz and Swartzman (1981). They developed a probabilistic age-structured model that was used to estimate variability in sustained yield at a range of levels of fishing effort. Results from their study indicate that, when recruitment is highly variable, significant differences in yield may be difficult to detect unless changes in the level of fishing effort are substantial. Thus, environmental variability, which produces these fluctuations in recruitment, might be viewed as advantageous in that it provides the fishery manager with considerable flexibility to incorporate socioeconomic

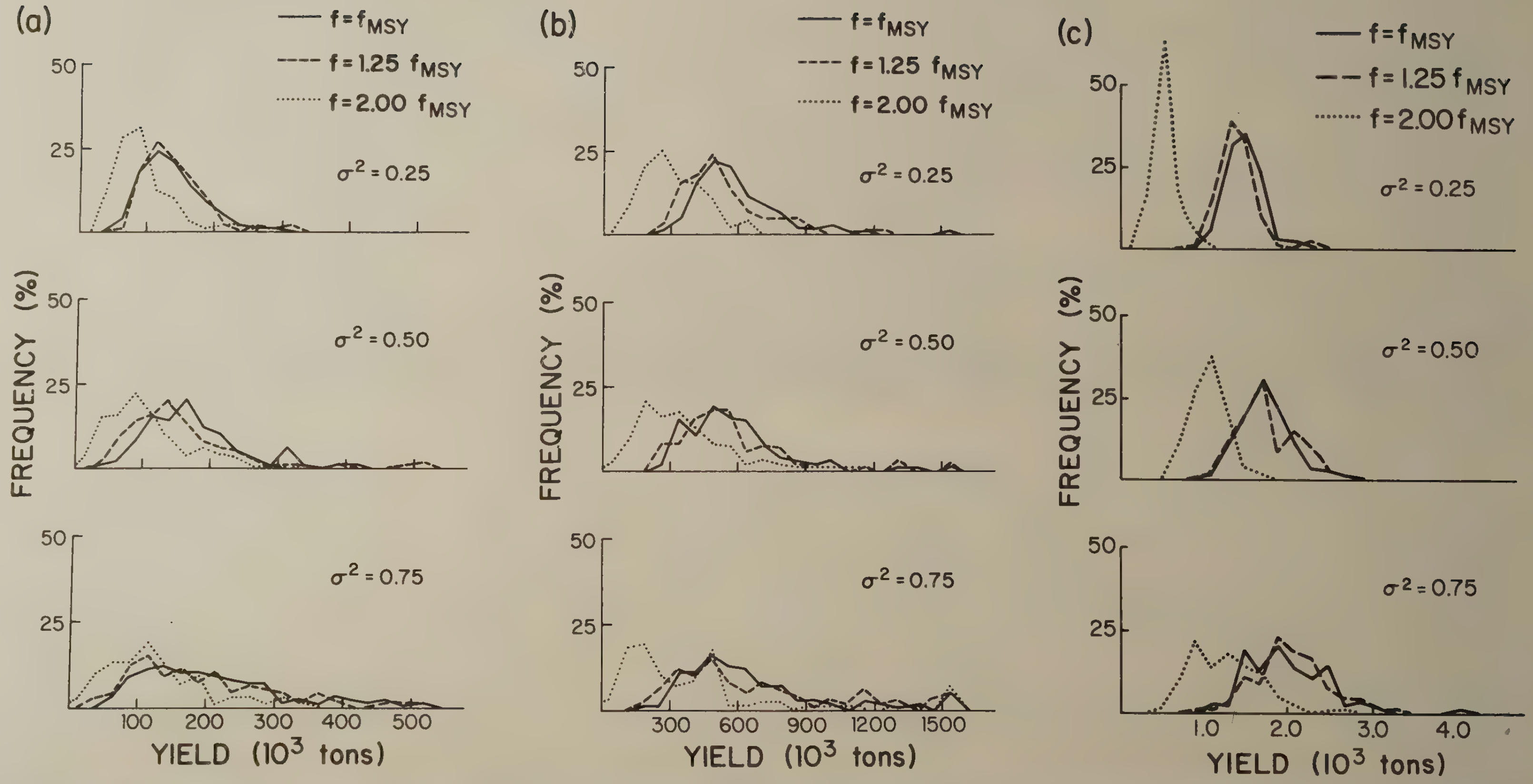

FIG. 2. Frequency distributions of harvest for (a) anchovy, (b) Atlantic menhaden, and (c) Pacific ocean perch obtained by maintaining effort at the level that produces maximum sustainable yield (f_{MSY}) or levels 25 and 100% greater than f_{MSY}. For each treatment combination, one of four frequency distributions of harvest at f_{MSY} was randomly selected for plotting. Environmental variability in the stock–recruitment relationship is given as σ^2.

factors into a management plan. Because these factors can rarely be ignored in policy formulation (Schoning 1984), it is encouraging to know that fishing effort may differ from a theoretically optimal level without resulting in a detectable reduction in harvest.

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References

ALLEN, K. R. 1973. The influence of random fluctuations in the stock–recruitment relationship on the economic return from salmon fisheries. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164: 350–359.

ANDERSON, E. D., AND A. J. PACIORKOWSKI. 1980. A review of the Northwest Atlantic mackerel fishery. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 175–211.

ANTHONY, V. C., AND G. WARING. 1980. The assessment and management of the Georges Bank herring fishery. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 72–111.

ARCHIBALD, C. P., D. FOURNIER, AND B. M. LEAMAN. 1983. Reconstruction of stock history and development of rehabilitation strategies for Pacific ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manage. 3: 283–294.

ARCHIBALD, C. P., W. SHAW, AND B. M. LEAMAN. 1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters, 1977–1979. Can. Tech. Rep. Fish. Aquat. Sci. 1048: 57 p.

BEVERTON, R. J. H. 1962. Long-term dynamics of certain North Sea fish populations, p. 242–264. *In* E. D. Le Cren and M. W. Holdgate [ed.] The exploitation of natural animal populations. John Wiley & Sons, New York, NY.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II, Mar. Fish. G. B. Minist. Agric. Fish. Food 19: 533 p.

CUSHING, D. H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. Int. Explor. Mer 33: 340–362.

DERISO, R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37: 268–282.

DERISO, R. B., AND T. J. QUINN II. 1983. The Pacific halibut resource and fishery in regulatory area 2: II. Estimates of biomass, surplus production, and reproductive value. Int. Pac. Halibut Comm. Sci. Rep. 67.

DOUBLEDAY, W. G. 1976. Environmental fluctuations and fisheries management. Int. Comm. Northwest Atl. Fish. Sel. Pap. 1: 141–150.

DRAGESUND, O., J. HAMRE, AND O. ULLTANG. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 43–71.

GETZ, W. M. 1980. Harvesting models and stock recruitment curves in fisheries management, p. 284–304. *In* W. M. Getz [ed.] Mathematical modelling in biology and ecology. Springer-Verlag, Berlin, Germany.

1985. Optimal and feedback strategies for managing multicohort populations. J. Optim. Theory Appl. 46(1).

GETZ, W. M., AND G. L. SWARTZMAN. 1981. A probability transition matrix model for yield estimation in fisheries with highly variable recruitment. Can. J. Fish. Aquat. Sci. 38: 847–855.

GULLAND, J. A. 1967. The effects of fishing on the production and catches of fish, p. 399–415. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. John Wiley & Sons, New York, NY.

1972. Population dynamics of world fisheries. Division of Marine Research, University of Washington, Sea Grant Program, Seattle, WA. 336 p.

1982. Why do fish numbers vary? J. Theor. Biol. 97: 69–75.

HENNEMUTH, R. C., J. E. PALMER, AND B. E. BROWN. 1980. A statistical description of recruitment in eighteen selected fish stocks. J. Northwest Atl. Fish. Sci. 1: 101–111.

HUANG, B., AND C. J. WALTERS. 1983. Cohort analysis and population dynamics of large yellow croaker in the China sea. N. Am. J. Fish. Manage. 3: 295–305.

JAKOBSSON, J. 1980. Exploitation of the Icelandic spring- and summer-spawning herring in relation to fisheries management, 1947–1977. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 23–42.

LARKIN, P. A. 1973. Some observations on models of stock and recruitment relationships for fishes. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164: 316–324.

LAUREC, A., A. FONTENEAU, AND C. CHAMPAGNAT. 1980. A study of the stability of some stocks described by self-regenerating stochastic models. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 423–438.

LAW, A. M., AND W. D. KELTON. 1982. Simulation modeling and analysis. McGraw-Hill, New York, NY. 400 p.

NELSON, W. R., M. C. INGHAM, AND W. E. SCHAAF. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. 75: 23–41.

NEWMAN, G. G., AND R. J. M. CRAWFORD. 1980. Population biology and management of mixed-species pelagic stocks off South Africa. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 279–291.

PETERMAN, R. M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38: 1113–1119.

PETERMAN, R. M., C. J. WALTERS, AND R. HILBORN. 1978. Pacific salmon management, p. 183–214. *In* C. S. Holling [ed.] Adaptive environmental assessment and management. John Wiley & Sons, Chichester, England.

POPE, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northwest Atl. Fish. Res. Bull. 9: 65–74.

REINTJES, J. W. 1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv. Circ. 320: 30 p.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SAS INSTITUTE, INC. 1982. SAS User's Guide: statistics, 1982 edition. SAS Institute, Incorporated, Cary, NC. 584 p.

SCHAAF, W. E. 1975. Status of the Gulf and Atlantic menhaden fisheries and implications for resource management. U.S. Natl. Mar. Fish. Serv. Mar. Fish. Rev. 37: 1–9.

1979. An analysis of the dynamic population response of Atlantic menhaden, *Brevoortia tyrannus*, to an intensive fishery. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 243–251.

SCHAAF, W. E., AND G. R. HUNTSMAN. 1972. Effects of fishing on the Atlantic menhaden stock: 1955–1969. Trans. Am. Fish. Soc. 101: 290–297.

SCHONING, R. W. 1984. Some impacts of resource data use in fisheries management. N. Am. J. Fish. Manage. 4: 1–8.

SHEPHERD, J. G. 1982. A versatile new stock–recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40: 67–75.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, NY. 312 p.

SISSENWINE, M. P., AND J. E. KIRKLEY. 1982. Fishery management techniques: practical aspects and limitations. Mar. Policy 6: 43–57.

STRONG, D. R. 1984. Density-vague ecology and liberal population regulation in insects, p. 184–192. *In* P. W. Price [ed.] A new ecology: novel approaches to interactive systems. Wiley, New York, NY.

SWARTZMAN, G. L., W. M. GETZ, R. C. FRANCIS, R. T. HAAR, AND K. ROSE. 1983. A management analysis of the Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model. Can. J. Fish. Aquat. Sci. 40: 524–539.

TROADEC, J. P., W. G. CLARK, AND J. A. GULLAND. 1980. A review of some pelagic fish stocks in other areas. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 252–277.

VAUGHAN, D. S. 1977. Confidence intervals on mortality rates based on the Leslie matrix, p. 128–150. *In* W. Van Winkle [ed.] Assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press, Elmsford, NY.

WALTERS, C. J., AND R. HILBORN. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

WALTERS, C. J., AND D. LUDWIG. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. 38: 704–710.

EARLY POSTNATAL GROWTH OF THE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN THE OFFSORE EASTERN TROPICAL PACIFIC

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ABSTRACT

Estimates of length at birth and early postnatal growth are made for the northern and southern populations of the offshore spotted dolphin in the offshore eastern tropical Pacific. Length at birth is estimated to be 85.4 cm for the northern population and 83.2 cm for the southern population. Analyses of series of monthly distributions of length revealed two cohorts born each year in the northern population, at least in the northern inshore part of its geographic range, but only one cohort born each year in the southern population. Growth curves fitted to the means of the monthly distributions of length gave estimates of length at 1 year of 126.2 and 132.6 cm and length at 2 years of 154.3 and 154.9 cm for the two cohorts in the northern population, and length at 1 year of 127.9 cm for the southern population. A growth curve fitted to lengths and ages (in dental growth layer groups) from the northern population gave estimates of lengths at 1 and 2 years of 123.0 and 143.0 cm, respectively.

The average growth rate of individual animals in a population is an important characteristic because of its correlation with other population parameters. In fisheries biology, two commonly employed techniques used to estimate growth rates are the aging of a sample of fish of known length and the following of a series of length distributions through time. These techniques allow the relationship between length and age (or relative age) to be applied to a much larger sample of fish, provided that the aged sample is a representative one.

For most species of fish, length-age relationships may be appropriate for the entire life of the animals, or at least for the period of interest to a commercial fishery. In marine mammals, however, length changes little, if at all, after attainment of physical maturity. Growth rates may change markedly even while the animal is maturing, being high for an initial period after birth and then declining quite rapidly. In delphinids, the growth rate has been found to be high in the first year, with animals typically increasing by 50-70% of their birth length (Sergeant 1962; Kasuya et al. 1974; Kasuya 1976; Miyazaki 1977; Hohn 1980; Perrin and Henderson 1984), but then declined rapidly in the second year. During this period, growth rates are high relative to the variability in age-at-length so that length distributions are distinguishable as separate age groups. Consequently, length-age relationships for these animals are most useful from birth until about 2 yr.

In this paper, we have used both the technique of following a series of length distributions from month to month and the technique of aging a sample of dolphins of known length to estimate the rate of growth in the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific (hereafter referred to as the offshore spotted dolphin). In neither of these two techniques did we have an absolute measure of age. Consequently, we have estimated length at birth independently and used this to fix time at birth. Growth curves were fitted to the length data by relative age and then length at birth was substituted in order to predict length-at-age.

THE SAMPLE

The field data and specimens used in the following analyses were collected by National Marine Fisheries Service (NMFS) and Inter-American Tropical Tuna Commission (IATTC) scientific technicians aboard commercial tuna purse seiners from 1968 to 1982. Procedures for collecting sample data and specimens have been described by Perrin et al. (1976). In all the following analyses, the data have been stratified into northern and southern popula-

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tions divided by lat. 1°S, based on a division selected by Perrin et al. (1979). Areas 1 and 2 in Figure 1 correspond to the region occupied by the southern offshore spotted dolphin and areas 3-8 correspond to the region occupied by the northern offshore spotted dolphin.

ESTIMATION OF LENGTH AT BIRTH

An accurate estimate of length at birth is important because it establishes a point through which any growth curve should pass. This extra degree of freedom allows greater accuracy in fitting growth curves and estimating growth rates. Neither of our methods of relating length to age, described below, allows us to fix absolute age so it is essential here for us to calculate an independent estimate of length at birth.

A commonly used method of estimating length at birth when a sufficient sample is available is to regress the percent postnatal at each length interval on length and to calculate the length at which 50% of the specimens are predicted to be postnatal. This method, using a linear model, has been employed to estimate length at birth for spotted dolphins (Perrin et al. 1976), for striped dolphins, *S. coeruleoalba*, (Miyazaki 1977), and for spinner dolphins, *S. longirostris*, (Perrin et al. 1977), and using a nonlinear model for spinner dolphins (Perrin and Henderson 1984). Another method commonly employed when a small sample is available is to estimate the average length at birth as the mean length of known neonates or the mean length of full-term fetuses and small calves combined. This method has been used to estimate length at birth for long-finned pilot whales (Sergeant 1962), for spotted dolphins (Kasuya et al. 1974), for bottlenose dolphins, *Tursiops truncatus*, (Ross 1977; Hohn 1980), and for

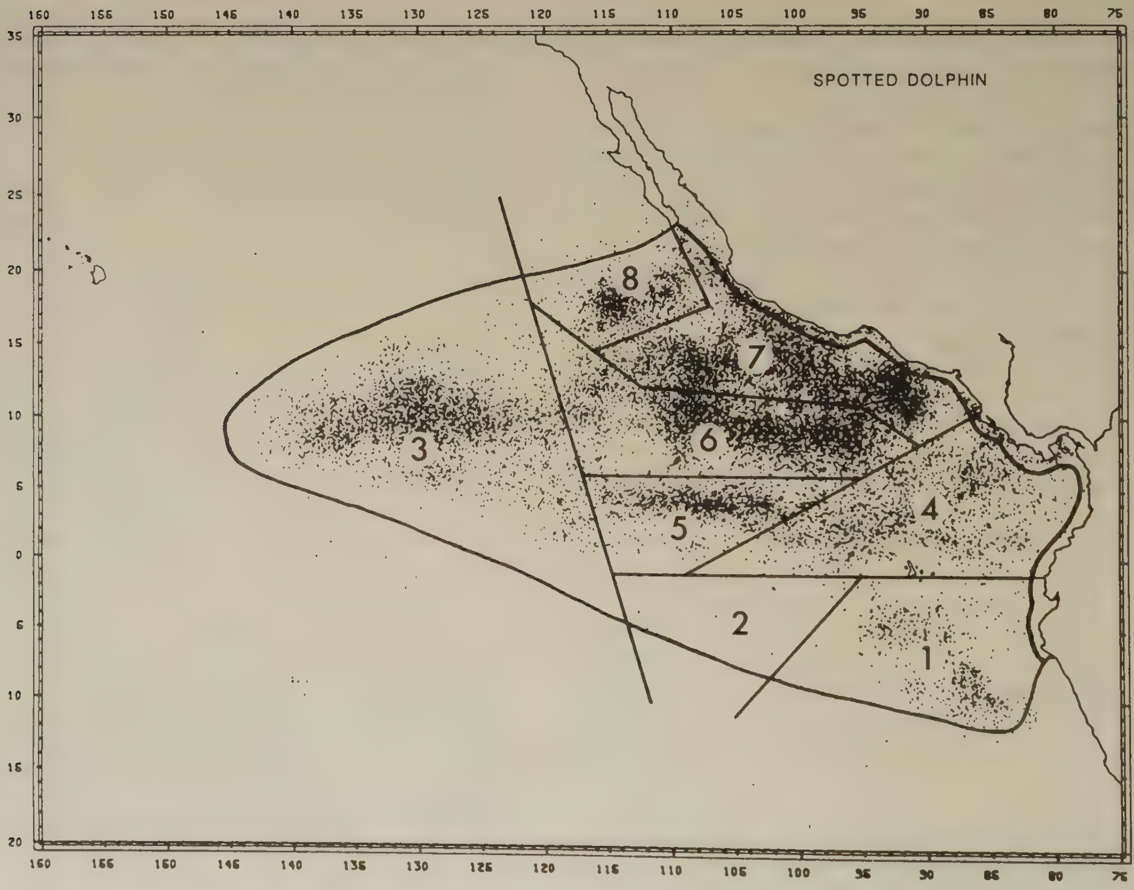

FIGURE 1.–Areas inhabited by the offshore spotted dolphin. The numbered regions refer to strata investigated in analyses of monthly distributions of length. In all analyses, the southern population is from areas 1 and 2, and the northern population is from areas 3 through 8.

the franciscana dolphin, *Pontoporia blainvillei*, (Kasuya and Brownell 1979).

Methods

The data used in this analysis were from all fetuses and calves sampled between 1973 and 1981 except for three specimens <68 cm identified as calves and one specimen of 91 cm identified as a fetus (n = 609). These four specimens were judged to have been misidentified. The data were stratified by area, north and south of lat. 1°S, and the northern sample was further stratified by the size of kill in each net set. Powers and Barlow (1979[3]) have shown that in net sets in which the kill of spotted dolphins from the northern offshore regions was ⩽40 (small-kill sets), about twice as many calves were killed as a proportion of the total kill as in sets where the kill was >40 (large-kill sets). This would introduce a bias in the estimate of length at birth in the regression procedure because about 90% of all northern specimens were from small-kill sets. The effect would be to underestimate length at birth because the ratio of calves to fetuses was too high in most of the sample. To investigate the extent of the bias, we calculated average length at birth for all northern specimens, for specimens from sets with kill ⩽40 and >40, and for specimens from sets with kill ⩽30 and >30 because the sample size for sets with kill >40 was small. The small sample available for southern specimens prevented any further stratification of the data.

Length at birth was estimated by fitting a logistic model to the percent postnatal at each length interval, weighted by the inverse of the binomial variance of each percentage, and estimated by calculating from the fitted curve the length at which 50% of the specimens were predicted to be postnatal. We also investigated linear and asymmetric logistic-type models.

Results

Figure 2 shows the length-frequency data for northern specimens from sets with kill ⩽40, and the logistic model fitted to the data. Figure 3 is the equivalent for northern specimens from sets with kill >40. Table 1 gives the results for all stratifications described above using the logistic model. Using the linear or asymmetric logistic-type models did not improve the fit and gave similar results.

Table 1 shows that the estimates of length at birth for northern specimens using the unstratified data (82.0 cm) and using specimens from sets with kill ⩽30 (81.6 cm) or ⩽40 (81.6 cm) are lower than the estimates using specimens from sets with kill >30 (84.6 cm) or >40 (85.4 cm), demonstrating that the bias resulting from an overrepresentation of calves in small-kill sets is significant. Furthermore, the estimate for kill >40 is higher than that for kill >30, indicated that the proportion of calves in the sample may still be a function of kill-per-set at this level. Further stratification to investigate whether or not estimates of length at birth continue to rise at higher thresholds of kill-per-set was not possible because of small sample size.

The estimate of length at birth for southern specimens is 83.2 cm. No stratification was possible because of the small sample.

Estimates of standard deviations of the estimates of length at birth are not given because, in fitting the logistic model, sums of squares were minimized for differences between observed and predicted percent postnatal and it was unclear how to calculate the standard deviations.

TABLE 1.—Estimates of length at birth stratified by number of offshore spotted dolphins killed per set. The range of length classes includes the last 0% postnatal length class and the first 100% postnatal length class.

	Sample size	Range (cm)	Length at birth predicted from the logistic model (cm)
Northern offshore spotted dolphin			
Unstratified data	586	71-92	82.0
Sets with kill ⩽30	321	73-92	81.6
Sets with kill ⩽40	384	71-92	81.6
Sets with kill >30	105	71-89	84.6
Sets with kill >40	36	78-89	85.4
Southern offshore spotted dolphin			
Unstratified data	23	78-85	83.2

Discussion

Our estimate of length at birth of 82.0 cm from the unstratified northern data is similar to that of Perrin et al. (1976), who estimated length at birth at 82.5 cm, based on a sample of 73 northern specimens (calves and fetuses) grouped into 3 cm intervals from 74 to 92 cm.

Estimates of length at birth in large-kill sets are less biased because of the overrepresentation of calves in small-kill sets. A future larger sample from large-kill sets may allow for additional stratification by kill-per-set, enabling estimates to be calculated

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[3] Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, Status of Porpoise Stocks Workshop, La Jolla, CA, 27-31 August 1979. Unpubl. MS.

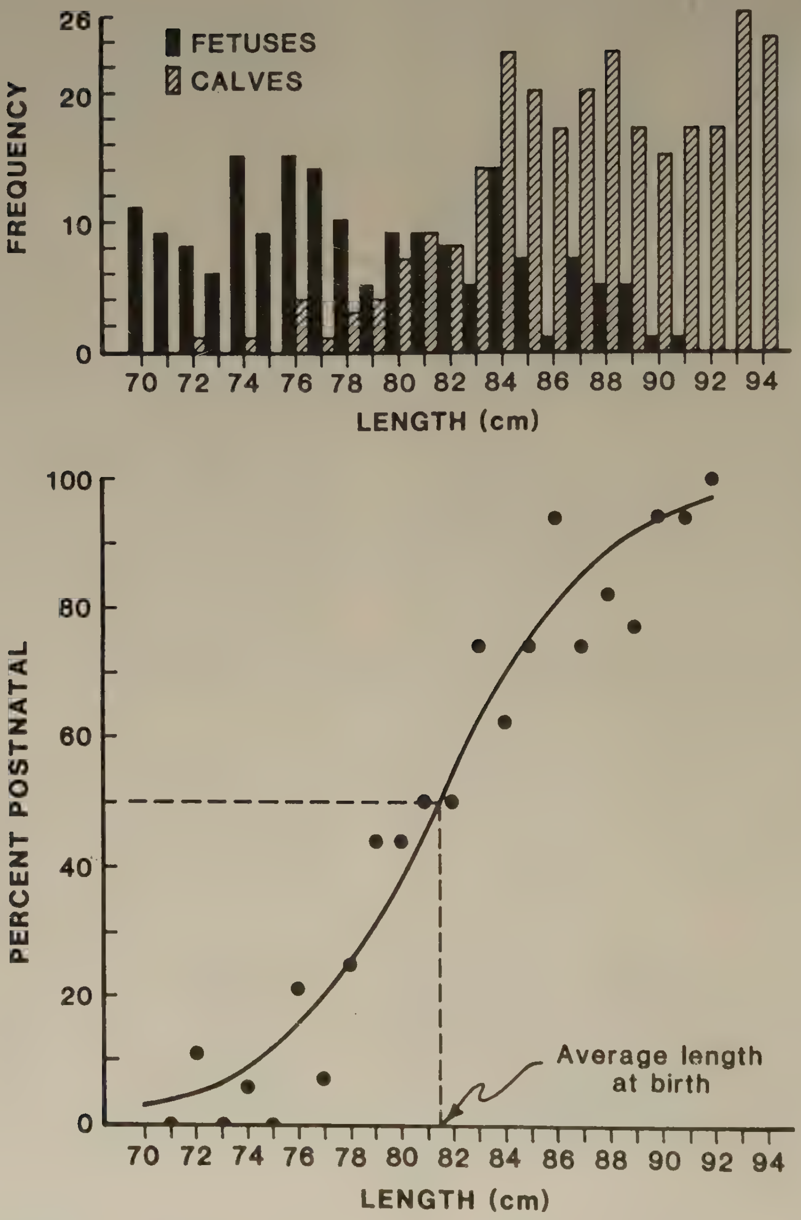

FIGURE 2.—Length-frequency data for specimens from sets with kill ≤40 grouped in 1 cm intervals for 163 fetuses and 221 calves from the northern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

using specimens from sets with higher levels of kill. It may then be possible to determine at what level of kill-per-set the estimate ceases to increase. Until additional data are available, we consider 85.4 cm to be the best estimate of length at birth in northern offshore spotted dolphins.

Our estimate of length at birth in the southern offshore spotted dolphin of 83.2 cm is more questionable because we were unable to stratify by kill-per-set. As adults, southern specimens are about 2.5 cm shorter than their northern counterparts (Perrin et al. 1979). This small, but statistically significant, difference may or may not imply that length at birth is smaller in the southern population. The small sample of 23 specimens used in our calculation of length at birth raises doubts concerning the

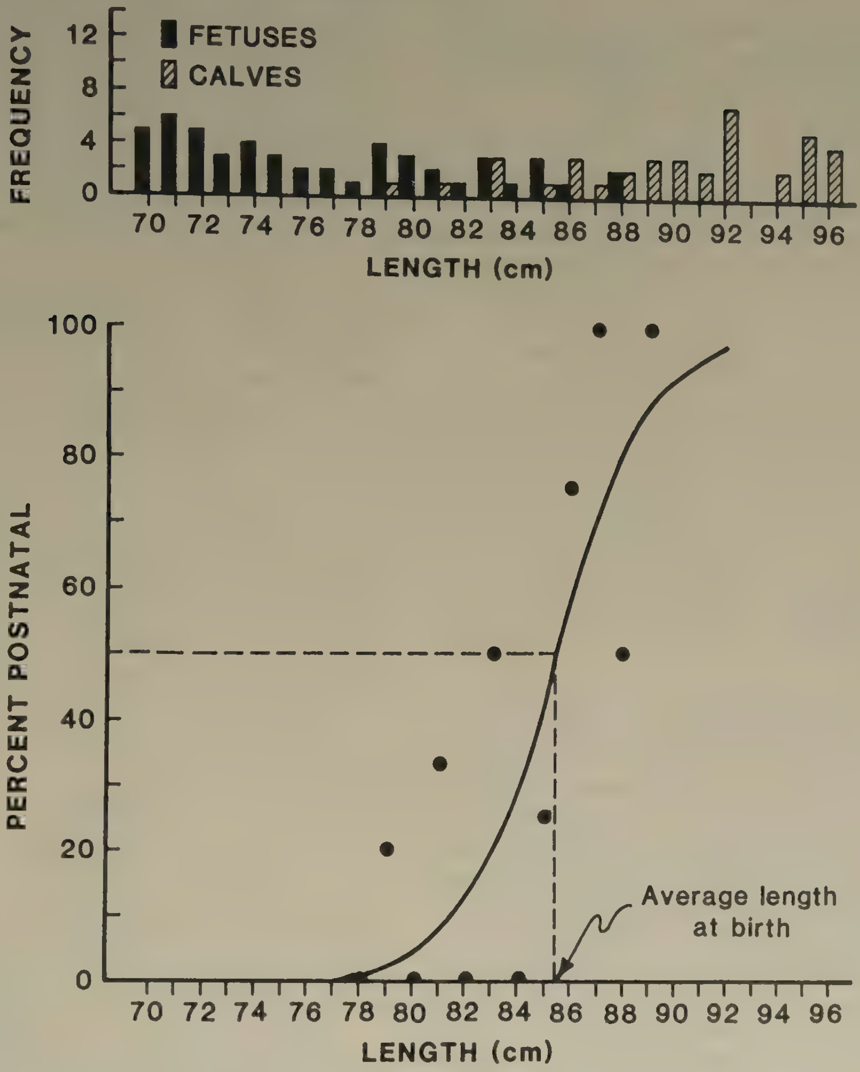

FIGURE 3.—Length-frequency data for specimens from sets with kill >40 grouped in 1 cm intervals for 21 fetuses and 15 calves from the southern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

accuracy of this estimate. For these reasons, we take the estimate from all southern specimens of 83.2 cm as our provisional best estimate of length at birth for southern offshore spotted dolphins while recognizing that this estimate may be biased downwards because of a possible overrepresentation of calves in the sample.

ESTIMATION OF LENGTH-AT-AGE USING ANALYSES OF MONTHLY DISTRIBUTIONS OF LENGTH

Perrin et al. (1976) used the technique of fitting a growth curve to the means of normal distributions fitted to length-frequency data by month to estimate the length of the offshore spotted dolphin at 1 yr of age. Perrin and Henderson (1984) used the same technique for the spinner dolphin. The technique is based on the assumption that breeding in these dolphins is seasonal and that a cohort of animals born at approximately the same time is characterized by a distribution of lengths, identifiable as a mode in the overall length distribution, which can be followed from month to month as mean length of the cohort increases. If there are sufficient data in each month, mean lengths can be followed from birth until growth slows to an extent that distributions of lengths from different cohorts cannot be distinguished. A growth curve can then be fitted to the monthly mean lengths.

Since the analysis of Perrin et al. (1976), the sample of measured lengths from offshore spotted dolphins has increased from about 3,500 to over 15,000. Consequently, we were able to analyze the available data more extensively than had been done previously.

Methods

Length measurements from all postnatal specimens, made between 1968 and 1982, were used in the analyses except for three specimens <68 cm which were judged to have been erroneously identified as calves. The data were stratified into eight areas based upon apparent hiatuses in distribution from examination of sightings and effort data (Fig. 1). Areas 1 and 2 comprise the southern population and areas 3-8 the northern population.

For the northern data, no consistency could be found in preliminary analyses of lengths when data from all areas were included. When area 3 was excluded, consistency was much improved. When areas 4 and 5 were also excluded, consistency was improved further for the months of February through June. This indicated that there were nonseasonal or seasonal but asynchronous elements in areas 3, 4, and 5 at least at certain times of the year. Consequently, in our analyses of northern data we used lengths from areas 6, 7, and 8 only for February through June and lengths from areas 4-8 for January and July through December. A similar situation occurred for the southern data where the elimination of area 2 improved consistency for January through May. In our analyses of southern data, therefore, we used lengths only from area 1 for these months.

The data were grouped in interval widths of 4 cm. This gave four possible ways of grouping the data because lengths were measured to the nearest whole centimeter. Each of these four groupings were investigated, there being no reason to prefer a starting point of the first interval as, for example, 76, 77, 78, or 79 cm.

A mixture of normal distributions was fitted to each data set using a version of the computer program NORMSEP (Hasselblad 1966). The program requires the number of distributions to be specified, and this was varied in order to determine the most likely number of distributions present. The model selected as most representative of the length-frequency data was that which gave the highest χ^2 value, and therefore the highest probability that a greater χ^2 value could be obtained by chance alone, and also gave biologically feasible results based on prior knowledge of delphinid growth. (Some model fits had a very high probability of a greater χ^2, but the mean lengths could not be accounted for by any reasonable regime of growth.)

We chose Laird's (1969) form of the Gompertz (1825) growth equation to fit to the monthly mean lengths. A linear model is clearly inadequate to describe growth except over a very short time period. We also investigated the use of the von Bertalanffy (1934) growth equation but found it to be less flexible than the Gompertz model.

Each model of growth was fitted to the mean lengths using the midpoint of the first month as time zero. In fact, this is not necessarily the time of birth so we fixed time of birth by substituting our estimate of length at birth into the fitted equation. Lengths at age were then calculated by substituting that age plus the difference between the midpoint of the first month and our calculated time of birth into the fitted equation.

Results

Northern Population

Figure 4 shows, as examples, the fitted mixture of normal distributions to the length-frequency data for August and October. The arrows indicate the positions of the means of the fitted distributions.

Table 2 shows the estimates of mean length of the fitted normal distributions for each month. The estimates are presented so that the increases from month to month can be clearly seen. The two final columns of Table 2 are mean lengths of the two distributions to the right of the length-frequency plots. These mean lengths are consistent from month to month. The table shows that there are actually two series of mean lengths: one beginning at 86.7 cm in September and continuing through columns 2 and 4 of the mean lengths, and the other beginning at 84.5 cm in April (the estimate of 92.7 cm for March is an anomaly for which we have no explanation) and continuing through columns 1, 3, and 5. These represent two cohorts born each year about 6 mo apart in the spring and autumn. Note that each series of mean lengths continues only for about 24 mo. This is because after this time growth has slowed to an extent that it is not possible to distinguish distributions of length from different cohorts. The

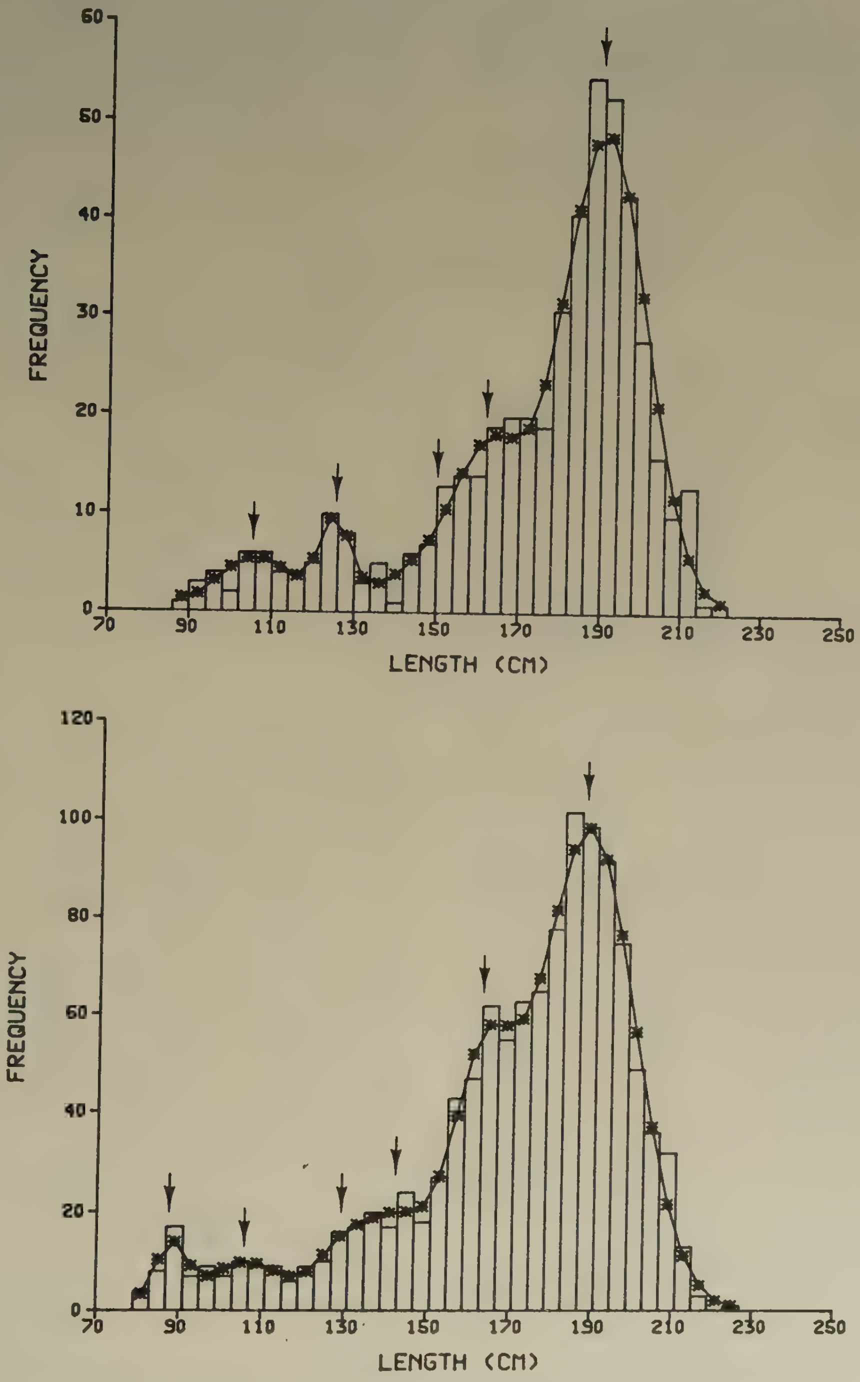

FIGURE 4.—Histograms of length and the fitted mixture of normal distributions for data for the northern offshore spotted dolphin in (A) August and (B) October. The arrows indicate the positions of the means of the fitted distributions.

mean length of 105.9 cm for June was not included in further analyses because its inclusion more than doubled the residual sums of squares for the model fit. We consider it an outlier.

Figure 5 shows Gompertz models of growth fitted separately to the mean lengths, excluding the 92.7 cm point for March, from columns 1, 3, and 5 (curve A) and, excluding the 105.9 cm point for June, from columns 2 and 4 (curve B) of Table 2. Time at birth and lengths at 1 and 2 yr were calculated as

TABLE 2.—Mean lengths of the fitted normal distributions for the northern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)						
September	536		86.7	105.0	129.4		161.3	186.9
October	1,159		87.9	106.3	129.4	142.7	163.1	188.8
November	616		91.9	113.9	129.6	145.7	159.4	187.7
December	223		97.5		127.7	149.9		187.4
January	2,926		102.9		142.4		161.9	187.4
February	2,772		104.1		140.7	151.8	161.5	186.3
March	866	[1]92.7	113.2	131.4			160.7	188.7
April	700	84.5	113.6		146.0		163.6	188.5
May	423	84.5	108.7	133.9	147.5		165.9	187.9
June	300	90.7	[1]105.9	135.5			165.2	189.5
July	266	91.8	118.0	136.1	150.8		164.5	190.1
August	486	105.7	125.1		151.8		162.6	190.5

[1] These mean lengths were not included in further analyses.

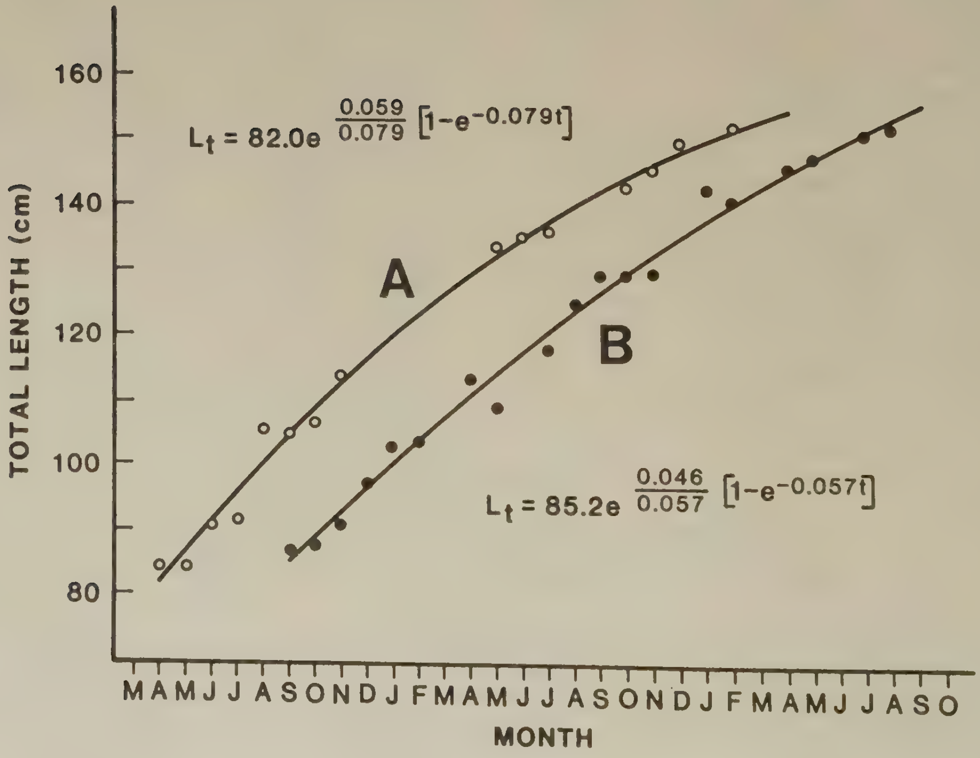

FIGURE 5.—Mean values of monthly distributions of length from data for the northern offshore spotted dolphin. The two curves represent two annual cohorts fitted separately by the Gompertz model of growth. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

described above with the following results:

	Growth curve A	*Growth curve B*
Fixed length at birth (estimated in this paper)	85.4 cm	85.4 cm
Estimated time of birth	May 9	September 11
Estimated length at 1 yr	132.6 cm	126.2 cm
Estimated length at 2 yr	154.9 cm	154.3 cm

Rates of growth as centimeters per month for the two fitted curves adjusted for length at birth are as follows:

	Rate of growth	
Months after birth	*Curve A*	*Curve B*
0	5.03	3.80
6	3.94	3.43
12	2.76	2.89
18	1.81	2.33
24	1.14	1.82

Southern Population

Table 3 shows the estimates of mean length of the fitted normal distributions for each month. For these data it is clear, apart from the mean lengths of 105.0 cm in January and 127.5 cm in May, that there is only one cohort born each year in the southern summer. As a result of this and the much smaller sample sizes, distributions of length could only be distinguished up to about 18 mo. The two final columns of Table 3 show the mean lengths of the two distributions to the right of the length-frequency plots. These are quite consistent from month to month, as with the northern data.

Figure 6 shows the Gompertz model of growth fitted to the mean lengths from columns 1 and 3 of Table 3. Time at birth and length at 1 yr were calculated as described above with the following results:

Fixed length at birth (estimated in this paper)	83.2 cm
Estimated time of birth	6 January
Estimated length at 1 yr	127.9 cm

Rates of growth for this fitted curve do not decrease from birth as they do for the northern population because the curve has a point of inflection at approximately 50 mo. The rates of growth at 0, 6, 12, and 18 mo after birth are 3.29, 3.72, 4.12, and 4.47 cm/mo, respectively.

TABLE 3.—Mean lengths of the fitted normal distributions for the southern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)				
December	47	81.0		123.5	165.7	187.9
January	254	87.0	[1]105.0	131.0	164.5	187.8
February	412	85.1		134.9	165.6	188.0
March	57	90.0		139.3		189.7
April	43	97.9		140.8	163.3	189.5
May	212	97.1	[1]127.5	144.3	157.7	182.6
June	42	99.0			163.8	185.3

[1] These mean lengths were not included in further analyses.

Discussion

There are several sources of variability in the estimates of mean length by month to which the growth models have been fitted. There is individual variation in time of birth, length at birth, and growth rate. The calving season may vary from year to year and area to area. The specimens which were measured are subject to the usual sampling variation. Sampling in a particular year may not have been random with respect to time in each month. Given these sources of variability, it is interesting that the results should appear so consistent.

The growth curves were fitted to the unweighted mean lengths. If the variation in the mean length of a distribution is considered to be due largely to sampling error, then there is a justification for a weighted regression. We believe that this is not necessarily the case and that the unweighted regressions represent the best descriptions of growth for these data. When weighted regressions were performed the fitted curves changed negligibly.

The most important potential problem is that the method relies upon being able to analyze a sample of data in which reproduction is seasonal and in which the timing of seasonality is constant. This analysis has shown that this may be difficult to achieve. Only by stratification of the data by area could consistent results be obtained. Stratification of the data by area improves the consistency of the series of mean lengths because offshore spotted dolphins appear to have different calving seasons depending upon the area of capture. In probability, this seasonality is not actually a function of area but of schools or groups of schools which tend to inhabit different areas with different environmental conditions. Thus, even with the best stratification scheme, there may always be asynchronous seasonal elements in a sample of data from any given area affecting the estimation of the mean lengths of the cohorts.

In this analysis we pooled the data from several years for our monthly samples, rather than attempt-

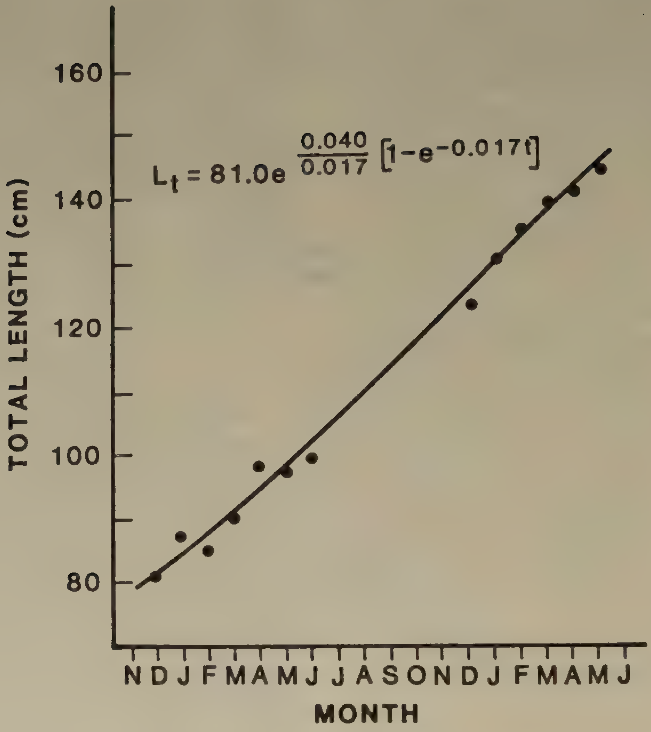

FIGURE 6.—Mean values of monthly distributions of length from data for the southern offshore spotted dolphin. The curve represents one annual cohort fitted by the Gompertz model of growth. The open circles were not included in the fitting of the curve. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

ing to follow actual cohorts of animals from individual years as did Perrin et al. (1976) in their analyses. Combining the data from several years introduces additional variation in the data if the timing of the calving season varies from year to year, but it increases sample sizes and minimizes bias caused by nonrandom timing of sampling within months. In addition, we are mainly interested in an average growth rate which is best estimated from several years of data.

Perrin et al. (1976) fitted a linear model to mean lengths estimated in the months of October 1972, January, February, March, and April through June 1973 from which they extrapolated to obtain an estimate of length at 1 yr of 147.5 cm for the northern offshore spotted dolphin. The authors recognized that this estimate was biased upwards because growth rates of delphinids do decrease in the first year and revised this estimate downwards based on aged specimens. We believe our analyses to be more accurate than those of Perrin et al. (1976) and our results to be a substantial improvement.

Barlow (1984) found an indication of two peak calving seasons for spotted dolphins north of the Equator, in the spring and autumn, but that the animals were born throughout the year. South of the Equator he found a single season peaking around April. These results are similar to ours but the timing of the southern season does not agree. The difference can be explained by Barlow's use of Perrin et al.'s (1976) growth curve which predicted a mean length of 138.0 cm for 1-yr-old animals. Our growth equations predict animals of this length to be from 14 to 16 mo old.

The two growth curves fitted to the mean lengths from the two cohorts in the northern region predict different lengths-at-age and are characterized by very different growth rates. It is possible that these two cohorts actually grow at different rates because of environmental factors, but we believe that the differences are more likely a result of variability in the data. We suggest, therefore, that the mean of the estimates from both growth curves be used for estimates of lengths-at-age for the northern offshore spotted dolphin.

For the southern population, the mean lengths of 105.0 and 127.5 cm for January and May, respectively, suggest that there may be two calving seasons in this area. At present, the sample size is too small to assess whether or not this is the case.

ESTIMATION OF LENGTH-AT-AGE USING GROWTH-LAYER-GROUP (GLG) AGING

Increments of tissue are deposited in teeth as a function of time. The most important incremental pattern in odontocete teeth is comprised of growth layer groups (GLGs), defined as "a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentine, cementum, or bone which is defined as a countable unit" (Perrin and Myrick 1980, p. 48-49). These GLGs are used for age determination in many species of odontocetes, as well as pinnipeds and sirenians (see review by Scheffer and Myrick 1980), but in most species no calibration of GLGs with absolute time is available. However, a few known-age captive and minimum-known-age captive bottlenose dolphins (Sergeant 1959; Sergeant et al. 1973; Hui 1978) and captive tetracycline-marked specimens of other species (*Lagenorhynchus obscurus*, Best 1976; *Delphinus delphis*, Gurevich et al. 1980; *S. longirostris*, Myrick et al. 1984) have provided evidence that the GLG as defined and calibrated by these workers represents an annual deposition pattern. In the absence of any known-age specimens of spotted dolphins, we have assumed that a GLG pattern similar to that described in the above species represents the same amount of time.

Methods

A sample of 800 males and 800 females, selected randomly from the specimens collected between 1973 and 1978, and all 312 female specimens collected in 1981 made up the sample of animals from which teeth were aged.

The teeth were decalcified in RDO[4], a commercial decalcifying agent, cut longitudinally into 24 μm thin sections using a freezing microtome, stained in haematoxylin, and mounted in 100% glycerin. Detailed procedures for the preparation technique and interpretation of GLGs are described by Myrick et al. (1983).

Teeth from each of the 1,600 specimens collected between 1973 and 1978 were "read" for age at least three times, to the nearest 0.1 GLG in young animals, by each of two readers over a period of 2 yr. The series of age estimates was averaged for each reader, and the resulting two mean age estimates were again averaged to produce a pooled mean age estimate (see Reilly et al. 1983). Only one age reading was made by each reader for the 312 specimens collected in 1981, and the mean of these two readings determined. For lack of a preference for one reader's estimates, growth rate analyses used the pooled mean and mean age estimates. Growth models were fit to the age-length data for males and females separately.

Growth rate was estimated by regressing length on number of GLGs (age) using Laird's (1969) form of the Gompertz model. The data were truncated at ≤3.0 GLGs in order to reduce the effects of older animals on our estimates of growth in the first 2 yr, in case the chosen model failed to describe growth adequately over a wider range of ages. Length at birth was fixed at the independently estimated value of 85.4 cm (see above).

Results

There was no difference in growth between males and females at this age. Therefore, the data were pooled. Figure 7 shows the Gompertz model of growth fitted to the pooled data. The model gives a predicted length of 123 cm (SD = 0.7 cm) at 1 yr and a predicted length of 143 cm (SD = 0.6 cm) at 2 yr. These standard deviations are underestimates because they do not incorporate variability in the age of individual specimens resulting from between reader differences.

Figure 7 also shows that lengths predicted by this model may be underestimated up to about 8 mo and overestimated from about 8 to 13 mo. For comparison with predicted length at 1 yr from the model, the mean length of specimens aged between 0.9 and 1.1 yr ($n = 24$) is 121 cm with a range of 101-140 cm.

The estimated monthly growth rate is 3.84 cm/mo initially, falling to 3.11 cm/mo at 6 mo, 2.33 cm/mo at 12 mo, 1.67 cm/mo at 18 mo, and 1.15 cm/mo at 24 mo.

Discussion

The accuracy of these length-at-age estimates depends upon the representativeness of the sample, the accuracy of the readings, the assumptions that 1 GLG equals 1 yr, and the adequacy of the growth model.

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The sample analyzed was a simple random sample, stratified only by sex, taken from all specimens collected between 1973 and 1978. These were themselves a sample of the animals killed incidental to fishing operations, which were a sample of the population. Although Powers and Barlow (fn. 2) have shown a bias towards a higher proportion of calves killed in purse seine nets, we have no reason to believe that the relationship between length and age is different in our sample than in the population.

Teeth were read as accurately as possible. Reilly et al. (1983) have investigated the precision of the readings but, without known-age animals, it is not possible to validate their accuracy.

Our assumption that 1 GLG equals 1 yr is based on captive, tetracycline-marked Hawaiian spinner dolphins (Myrick et al. 1984) a distantly related species. Known-age, captive or marked spotted dolphins are not available for direct GLG calibration. If differences are found between GLG in spotted and spinner dolphin teeth when data from known-age spotted dolphins are available, these estimates of growth based on GLGs will need to be revised.

It is often assumed that when one GLG is deposited each year the first GLG begins with the neonatal line immediately at birth and ends precisely 1 yr later. Yet it is possible, as suggested by Perrin et al. (1977) for *S. longirostris*, that the first GLG is not always complete. Teeth from young, known-age dolphins from the same stock born at different times during the year are needed to address this question.

It is also possible that the neonatal line may not be deposited immediately at the time of birth. In bottlenose dolphins, stranded on the mid-Atlantic coast of the United States, variability has been found in the time of deposition of the neonatal line in 18 neonatal specimens (Hohn unpubl. data). These specimens were identified as neonates because they lacked the umbilicus (indicating that the calf was not stillborn) and their dorsal fin and flukes were folded (Tavolga and Essapian 1957). Some of these stranded specimens showed no neonatal line while others had part of a neonatal line deposited. Similarly, in our sample of offshore spotted dolphins from northern areas there is not neonatal line in some postnatal specimens so that the amount of time since birth is unknown. This difference in timing of neonatal line deposition may be due to individual variation in tooth growth and mineralization or small difference in gestation time.

The precise timing of the deposition of the first

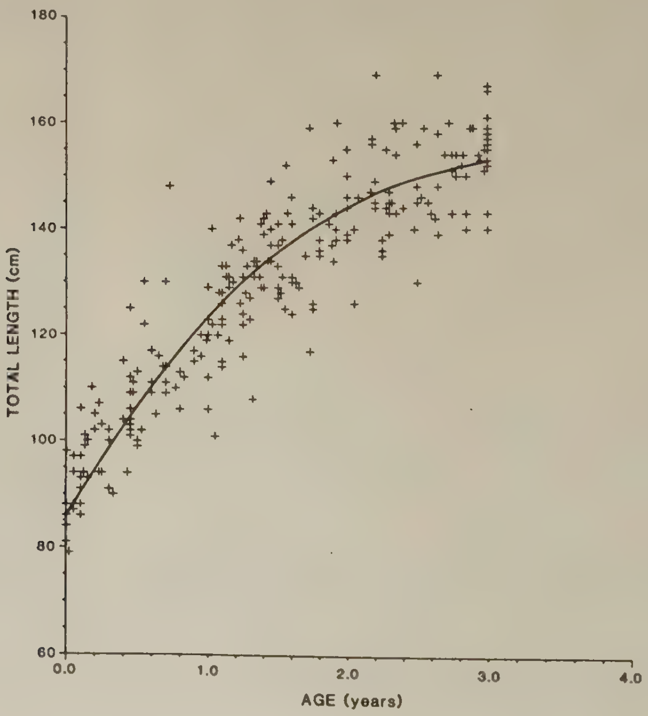

FIGURE 7.—Length-age [GLGs, (growth layer groups), pooled mean estimates] data for northern offshore spotted dolphins up to 3.0 GLGs, and the fitted Gompertz model of growth.

GLG (beginning with the neonatal line) is important in estimates of age in young animals. For a specimen estimated to be 0-yr-old based on GLGs but which is known not to be a neonate, the age must necessarily be an underestimate of the actual age of that specimen, and, consequently, the average length of "0-yr-olds" would be greater than the average length of new-born specimens. When the Gompertz model (with L_0 not fixed) is fitted to the age data, the predicted length at age 0 is 89.6 cm, 4.2 cm higher than the length-at-birth estimate. The age at which the predicted length is 89.6 cm when L_0 is fixed at 85.4 cm is about 0.1 GLGs. This indicates a possible bias of about 0.1 GLGs for young animals. However, this difference between predicted length for fits of the model with fixed and floated L_0 diminishes rapidly and at 0.7 GLGs predicted length is 114.0 cm for both models.

The Gompertz model appears to be generally suitable in describing the early growth of the offshore spotted dolphin based on GLG readings. However, the pattern of points around the fitted line in Figure 7 up to about 1.1 GLGs indicates that growth during this period may not be adequately described by a single curve. This pattern may be a result of either sampling variation or errors in reading, but it may be due to changes in growth rate during this period resulting from changes in food intake. Perrin et al. (1976) have estimated that weaning occurs at about 11 mo in the offshore spotted dolphin so that during the period from about 8 to 13 mo, milk intake will be decreasing and the intake of solid food will be increasing. Growth rates may well reflect these changes. If this is the case, a two-cycle model may describe growth more accurately during this period. Such an approach was used by Perrin et al. (1976, 1977) in spotted and spinner dolphins, respectively, to describe a secondary surge in the growth of pre-adult animals.

CONCLUDING REMARKS

Our analyses have produced different estimates of growth rates and lengths-at-age from two different techniques. The reliability of fitting growth curves to series of means of identifiable distributions of length by month depends primarily upon being able to select a sample in which breeding is both seasonal and synchronous from year to year. The reliability of fitting growth curves to length-age data as determined by counting GLGs depends primarily upon the validity of the assumption that 1 GLG is equivalent to 1 yr. We believe that neither technique is sufficiently reliable to be labelled as the "best" method or to try to calibrate the other. Rather, our analyses underline the need for the analysis of data collected from known-age animals of these populations. However, we do believe that the estimates of growth rates and lengths-at-age presented here are the best currently available for offshore spotted dolphins from the eastern tropical Pacific.

ACKNOWLEDGMENTS

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LITERATURE CITED

BARLOW, J.
1984. Reproductive seasonality in pelagic dolphins, (*Stenella* spp.): Implications for measuring rates. *In* W. F. Perrin, D. P. DeMaster, and R. L. Brownell (editors), Reproduction in cetaceans, p. 191-198. Rep. Int. Whaling Comm. Spec. Issue 6.

BEST, P. B.
1976. Tetracycline marking and the rate of growth layer formation in the teeth of a dolphin, *Lagenorhynchus obscurus*. S. Afr. J. Sci. 72:216-218.

GOMPERTZ, B.
1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of Life Contingencies. Philos. Trans. R. Soc. Lond. 115:513-585.

GUREVICH, V. S., B. S. STEWART, AND L. H. CORNELL.
1980. [1981]. The use of tetracycline in age determination of common dolphins, *Delphinus delphis*. *In* W. F. Perrin and A. C. Myrick, Jr. (editors), Age determination of toothed whales and sirenians, p. 165-170. Rep. Int. Whaling Comm. Spec. Issue 3.

HASSELBLAD, V.
1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.

HOHN, A. A.
1980. Age determination and age related factors in the teeth of western North Atlantic bottlenose dolphins. Sci. Rep. Whales Res. Inst., Tokyo 32:39-66.

HUI, C.
1978. Reliability of using dentine layers for age determination in *Tursiops truncatus*. U.S. Dep. Commer., Natl. Tech. Inf. Serv., PB288444, 25 p.

Kasuya, T

1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Sci. Rep. Whales Res. Inst., Tokyo 28:73-106.

Kasuya, T., and R. L. Brownell, Jr.

1979. Age determination, reproduction, and growth of Franciscana dolphin *Pontoporia blainvillei*. Sci. Rep. Whales Res. Inst., Tokyo 31:45-67.

Kasuya, T., N, Miyazaki, and W. H. Dawbin.

1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst., Tokyo 26:157-226.

Laird, A. K.

1969. The dynamics of growth. Res. Dev. 20(8):28-31.

Miyazaki, N.

1977. Growth and reproduction of *Stenella coeruleoalba* off the Pacific coast of Japan. Sci. Rep. Whales Res. Inst., Tokyo 29:21-48.

Myrick, A. C., Jr., E. W. Shallenberger, I. Kang, and D. B. MacKay.

1984. Calibration of dental layers in seven captive Hawaiian spinner dolphins, *Stenella longirostris*, based on tetracycline labeling. Fish. Bull., U.S. 82:207-225.

Myrick, A. C., Jr., A. A. Hohn, P. A. Sloan, M. Kimura, and D. Stanley.

1983. Estimating age of spotted and spinner dolphins, (*Stenella attenuata* and *Stenella longirostris*) from teeth. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-30, 17 p.

Perrin, W. F., J. M. Coe, and J. R. Zweifel.

1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

Perrin, W. F., and J. R. Henderson.

1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. *In* W. F. Perrin, D. P. DeMaster, and R. L. Brownell (editors), Reproduction in cetaceans, p. 417-430. Rep. Int. Whaling Comm. Spec. Issue 6.

Perrin, W. F., D. B. Holts, and R. B. Miller.

1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75:725-750.

Perrin, W. F., and A. C. Myrick, Jr. (editors).

1980. [1981]. Age determination of toothed whales and sirenians. Rep. Int. Whaling Comm. Spec. Issue 3, 229 p.

Perrin, W. F., P. A. Sloan, and J. R. Henderson.

1979. Taxonomic status of the 'south-western stocks' of spinner dolphin *Stenella longirostris* and spotted dolphins *S. attenuata*. *In* W. F. Perrin and A. C. Myrick, Jr. (editors), Age determination of toothed whales and sirenians, p. 175-184. Rep. Int. Whaling Comm. 29.

Reilly, S. B., A. A. Hohn, and A. C. Myrick, Jr.

1983. Precision of growth layer group ageing of spotted dolphins. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-35, 27 p.

Ross, G. J. B.

1977. The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. Ann. Cape Prov. Mus. (Nat. Hist.) 11:135-194.

Scheffer, V. B., and A. C. Myrick, Jr.

1980. [1981]. A review of studies to 1970 of growth layers in the teeth of marine mammals. *In* W. F. Perrin and A. C. Myrick, Jr. (editors), Age determination of toothed whales and sirenians, p. 51-64. Rep. Int. Whaling Comm. Spec. Issue 3.

Sergeant, D. E.

1959. Age determination of odontocete whales from dentinal growth layers. Norsk Hvalfangst-Tid. 48:273-288.

1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Fish. Res. Board Can., Bull. 132, 84 p.

Sergeant, D. E., D. K. Caldwell, and M. C. Caldwell.

1973. Age, growth, and maturity of bottlenose dolphin (*Tursiops truncatus*) from northeast Florida. J. Fish. Res. Board Can. 30:1009-1011.

Tavolga, M. C., and F. S. Essapian.

1957. The behavior of the bottle-nosed dolphin (*Tusiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. Zoologica (N.Y.) 42(1):11-31.

von Bertalanffy, L.

1934. Untersuchungen über die Gesetzlickeit des Wachstums. Wilhelm Roux' Arch. Entwichlungsmech. Org. 131:613.

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REPRODUCTIVE MATURITY AND SEASONALITY OF MALE SPOTTED DOLPHINS, *STENELLA ATTENUATA*, IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

We estimated age at attainment of sexual maturity and examined reproductive seasonality for male spotted dolphins, *Stenella attenuata,* from the eastern tropical Pacific Ocean. Maturity was determined by histological examination of testes. Average age at sexual maturation was 14.7 yr (the mean of two readers' age estimates). Testis and epididymis weight and seminiferous tubule diameters were reliable indicators of maturity, whereas age, length and color phase were less reliable. Seasonality was determined by changes in testis and epididymis weight, relative quantity of spermatids and spermatozoa, and lumen diameter, as well as an index of testis development (weight of the right testis and epididymis divided by length of the right testis). Testis and epididymis weights and index values peaked in July and August, midway between two predicted mating seasons for the northern offshore stock, but spermatozoa levels were elevated during the predicted breeding seasons.

Key words: spotted dolphin, *Stenella attenuata,* reproduction, sexual maturity, seasonality, testis histology.

Estimates of age and size of dolphins at sexual maturation are useful for comparative biological studies and can provide information for management of populations that are subject to mortality by man. The determination of sexual maturity in male dolphins must initially be based on histological examination of cross-sections of gonadal tissue, which is more accurate than gross observation. From this examination, states of maturity can be correlated with more readily available life history data such as body length, testis weight and age. For spotted dolphins, maturation has been correlated with an ontogenetic series of color phases (Perrin 1969, Kasuya *et al.* 1974). In addition, seasonal trends in testis development can identify or corroborate probable mating seasons.

In this paper, we describe states of maturity (immature, pubertal and mature) for a sample of male spotted dolphins based on testis histology. After defining maturity histologically, we calculated age and body length at attainment of sexual maturity. We also describe relationships between testis weight, testis length, seminiferous tubule diameter, body length, age and color phase as well as seasonal changes in testis tissue characteristics.

MATERIALS AND METHODS

The Samples

We used spotted dolphin specimens that had been collected by biological technicians from the National Marine Fisheries Service (NMFS) and Inter-American Tropical Tuna Commission aboard tuna purse-seine vessels in the eastern tropical Pacific (ETP). Collection procedures were described by Perrin *et al.* (1976). Specimens from both the northern and southern offshore stocks were examined (for stock definition, *see* Perrin *et al.* 1985).

We used two subsets of the sample from the northern offshore stock. The first, the life history sample, included all specimens collected from 1973 to 1982 for which testis and epididymis weights were recorded (n = 3,061). Generally, only the right testis and epididymis were collected (all testes analyses in this study refer to the right testis only). The samples were preserved in formalin and weighed in the laboratory. The second subset was divided into two samples (Fig. 1): (1) the aged sample consisted of 800 northern offshore specimens that were randomly selected from the 1973–1978 portion of the life history sample for an age distribution study; (2) the histology sample (n = 269) comprised all fused and mottled specimens for which age, testis and epididymis weight, and preserved testis tissue were available; it included 244 specimens drawn from the aged sample and 25 from the study by Perrin *et al.* (1976). Only the specimens from the random aged sample were used to estimate age and length at maturation. The techniques for tooth preparation and age determination were described by Myrick *et al.* (1983). The age estimates used in these analyses were described by Reilly *et al.* (1983). All age estimates for specimens in the aged sample were made independently by two readers. Although there are reader differences in the age estimates, we have no reason to expect that one set of estimates is more accurate than the other. Therefore, both sets are used to estimate age at maturation.

We also examined reproductive seasonality in testis and epididymis weight for the southern stock using criteria used to define maturity in the northern offshore specimens.

The Analyses

The testis tissue was thin-sectioned (6 μm), stained with haematoxylin and eosin, and examined for the presence and abundance of spermatogonia, spermatocytes, spermatids and spermatozoa, as well as for relative quantity of interstitial tissue, tubule elongation, lumen size and seminiferous tubule elon-

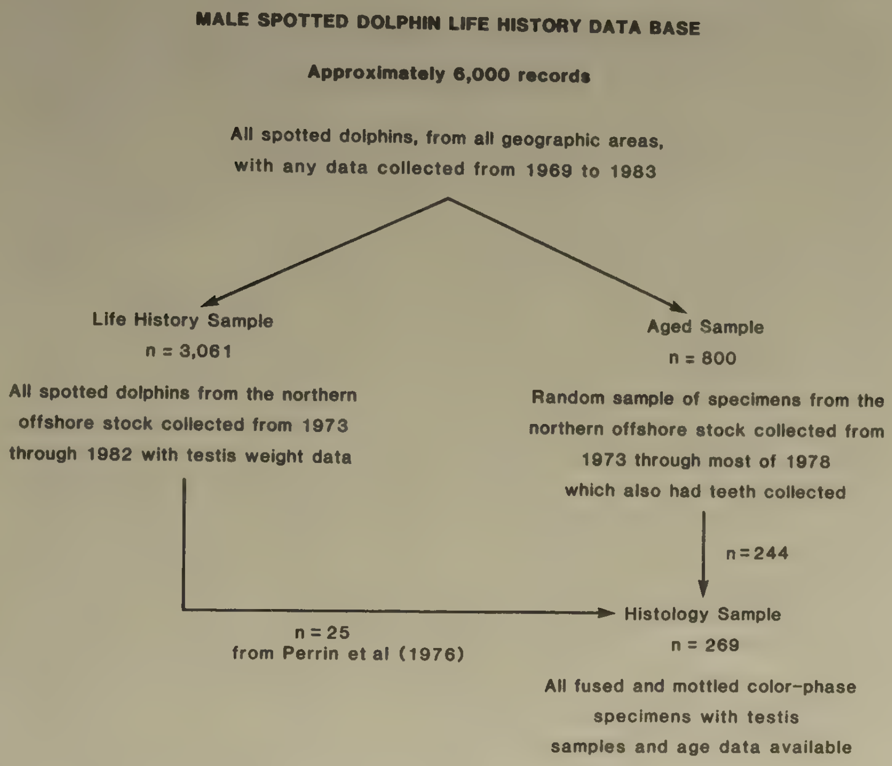
MALE SPOTTED DOLPHIN LIFE HISTORY DATA BASE
Approximately 6,000 records
All spotted dolphins, from all geographic areas, with any data collected from 1969 to 1983
Life History Sample
n = 3,061
All spotted dolphins from the northern offshore stock collected from 1973 through 1982 with testis weight data
Aged Sample
n = 800
Random sample of specimens from the northern offshore stock collected from 1973 through most of 1978 which also had teeth collected
n=244
n = 25
from Perrin et al (1976)
Histology Sample
n = 269
All fused and mottled color-phase specimens with testis samples and age data available

Figure 1. Relationships among the samples described in the text.

gation. We categorized the interstitial tissue according to the amount of tissue present: little, moderate or abundant in quantity. (Some care must be used in interpreting these categories since some interstitial tissue shrinkage occurs during fixation.) We categorized the tubules according to the degree of elongation: none, some or extensive. Lumen size was scored as none, small, medium and large. Tubules with lumen size "none" were those that were densely packed with tissue and spermatogonia. Small lumens were generally filled with tissue although the tissue was less densely packed than in those with no lumen present, partly because the tubules were enlarged. Medium lumen size had less tissue present than in small lumens and the tissue had separated in the center to leave a small, clear open space. Large lumens contained essentially no intra-tubular tissue. Only the products of spermatogenesis, especially spermatids and spermatozoa, were observed in the central lumen, or a large space devoid of tissue occupied nearly the entire tubule. Seminiferous tubule diameter was measured using an ocular micrometer and taken as the mean of at least 5 representative cross-sections of tubules that were circular in appearance.

Three states of sexual maturity were defined: immature, pubertal and mature. These were based on criteria of testes maturation used for other mammals (Charny *et al.* 1952, Laws 1956*a*, Hirose and Nishiwaki 1971, Bloom and

Fawcett 1975, Collet and Saint Girons 1984). The primary criterion was the presence or absence of cells in the various stages of spermatogenesis. In specimens classified as immature, seminiferous tubules contained primarily spermatogonia and had no lumen or cells of later stages. The tubules were imbedded in abundant interstitial tissue, densely packed, circular in cross-section and not elongated. The tubules were distinctly smaller than those in pubertal or mature specimens. In specimens classified as pubertal, the seminiferous tubules had slight elongation (although they were still relatively small in diameter), there was little interstitial tissue in the space between tubules, the lumen was small and empty and, most importantly, spermatogonia, spermatocytes and (rarely) spermatids were present. There were no spermatozoa. The primary criterion of sexual maturity was the presence in the tubules of spermatogonia, spermatocytes, spermatids and often spermatozoa. If any spermatozoa were found, the specimen was considered to have been mature. When all stages of spermatogenesis were present, they were in sequential order, by stage of development, from the tubule epithelium to the lumen. Although the presence of spermatozoa explicitly indicates sexual maturity, some specimens with no spermatozoa were also considered mature on the basis of other criteria: distinctly elongated seminiferous tubules with large diameters, a large lumen and little interstitial tissue.

After we had identified maturity states histologically, we estimated the fraction of immature, pubertal and mature specimens within each of the five ontogenetic color phases: neonatal (no spots), two-tone (no spots), speckled (dark spots ventrally), mottled (light spots ventrally and dorsally) and fused (ventral spots convergent) (Perrin 1969).

We calculated an index of testis development (right-testis and epididymis weight in grams divided by right-testis length in millimeters), which defines maturity in terms of unit of testis weight per unit of testis length, to remove variability in testis weights among specimens of different sizes. We calculated the index for specimens from the histology sample for which right-testis lengths were available (*n* = 268) and applied the results to the life history sample to estimate maturity.

On the basis of the histology results, we used a non-parametric method (Cooke[1]) to estimate the age at which males attain sexual maturity. The mean age of attainment of sexual maturity was calculated as

$$\bar{X}_{ASM} = \sum_{i=0}^{k} P_i \qquad (1)$$

where

i = age class interval from i to $i + 1$ yr
P_i = proportion of immature individuals in age class i
k = age class of oldest immature individual.

The formula given by Cooke differs in that he assigns ages to the midpoint of age-class intervals, thus subtracting 0.5 from the above sum. Standard errors

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[1] Cooke, J. G. Manuscript. The estimation of mean ages of sexual maturity from age samples. Paper SC/36/022 presented to the International Whaling Commission Scientific Committee, Cambridge, U.K., June 1984.

Table 1. Estimated age, length and gonadal characteristics by state of maturity in *S. attenuata*. Sample sizes were 61 immature, 27 pubertal and 181 mature.[1]

Characteristic and maturity state	Mean	Standard error	Range
Estimated age (years)			
Immature	11.3	0.4	4.0–19.2
Pubertal	16.7	0.7	10.0–24.0
Mature	22.4	0.3	11.8–37.0
Total body length (cm)			
Immature	175.0	0.9	154.0–188.0
Pubertal	186.0	1.7	174.0–204.0
Mature	200.4	0.6	175.0–231.0
Seminiferous tubule diameter (μm)			
Immature	46.1	0.9	29.9–68.8
Pubertal	77.1	3.8	51.8–135.0
Mature	169.1	2.6	92.5–276.0
Right-testis weight (g)			
Immature	18.7	1.1	6.9–52.0
Pubertal	70.2	6.9	21.0–155.0
Mature	498.4	18.8	127.0–1,448.0
Right-testis length (mm)			
Immature	95.6	2.2	64.0–142.0
Pubertal	146.2	6.0	100.0–208.0
Mature	250.1	3.1	113.0–370.0
Index of testis development			
Immature	0.2	0.0	0.1–0.4
Pubertal	0.5	0.0	0.2–0.9
Mature	1.9	0.1	0.7–4.2

[1] Sample size was 60 (rather than 61) for total length of immatures and 180 (rather than 181) for testis length and index of testis development.

in estimates of ASM were calculated from Cooke's variance formula (Cooke, equation 2). We also fit a three-parameter sigmoid curve to the proportion of mature specimens within each age class (regression weights determined by the inverse of the binomial variances):

$$P(X) = \frac{e^{(P1+P2(X)^{P3})}}{1 + e^{(P1+P2(X)^{P3})}} \tag{2}$$

where P(X) is the proportion mature within each age class, X, and P1, P2 and P3 are parameter values.

The body length at which males attain sexual maturity was determined using Cooke's method applied to the proportion of mature males within 5-cm body-length groups.

We analyzed the data for evidence of seasonal trends. The histology sample

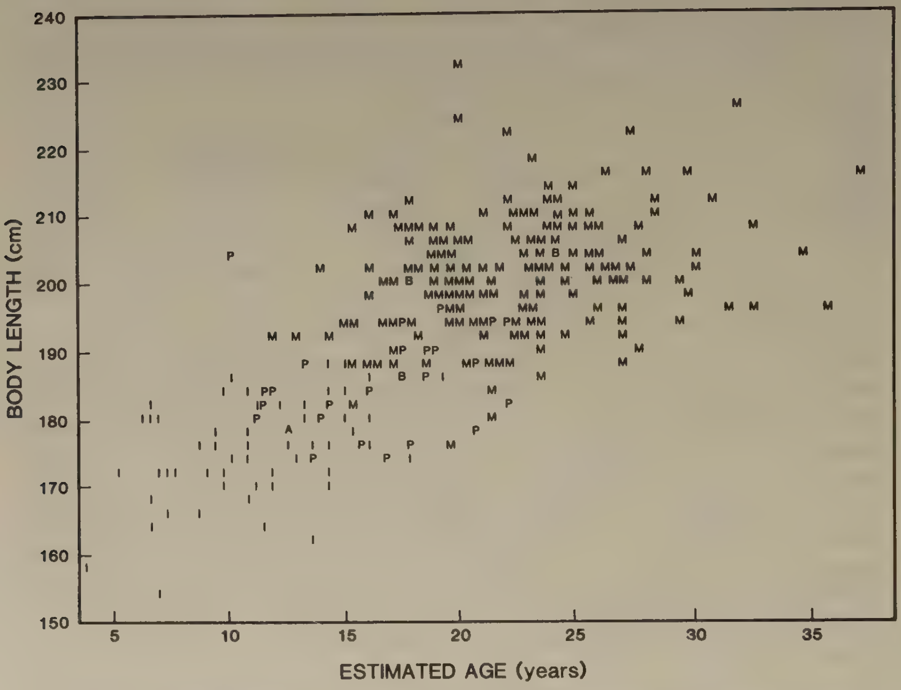

Figure 2. Body length as a function of age. I = immature, P = pubertal, M = sexually mature, A = overlapping immature and pubertal, B = overlapping pubertal and mature.

was examined for seasonal trends in mean tubule diameter, mean lumen diameter and the relative number of spermatids and spermatozoa. Trends in testis and epididymis weights for both the northern and southern stocks in the life history sample were also examined.

We examined the relation between right-testis weights with and without epididymides for the specimens collected in 1982 (the only year for which such data were available).

Results

Of the 269 specimens in the histology sample, 61 were classified as immature, 27 as pubertal and 181 as mature. The mean values for seminiferous tubule diameter, right-testis and epididymis weight, body length, and age were all significantly greater for mature specimens than for immature and pubertal animals (t-tests, $P < 0.001$, Table 1).

Overlap was substantial for age and body length between immature, pubertal and mature specimens (Table 1, Fig. 2). There was less overlap for testis and epididymis weight; testis weight exceeded 140 g in only two non-mature dol-

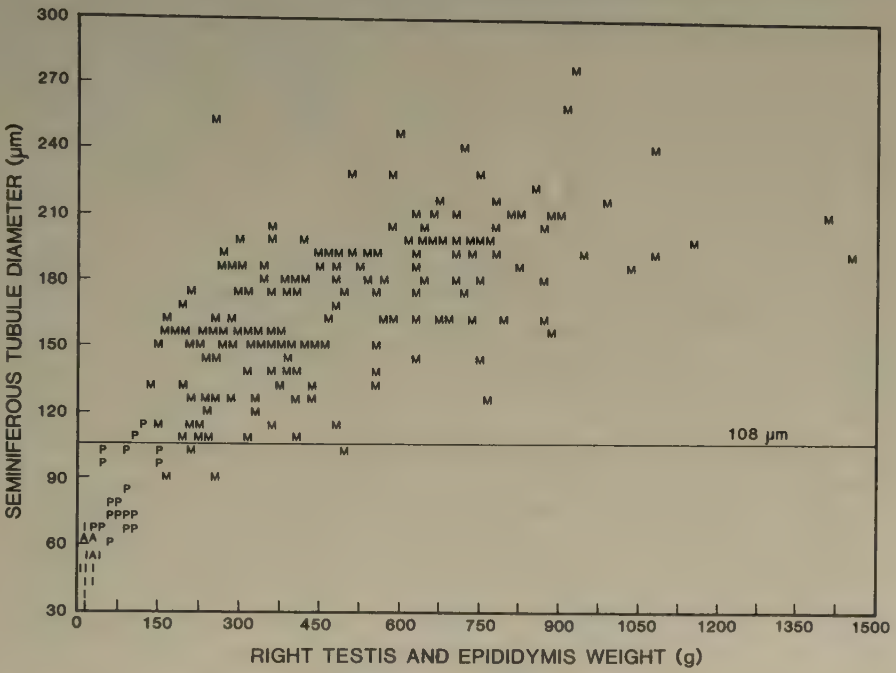

Figure 3. Seminiferous tubule diameter as a function of testis + epididymis weight; 108 µm is the approximate median seminiferous tubule diameter at attainment of sexual maturity. See Figure 2 for data codes.

phins (both pubertal) and only one mature specimen had a testis weight less than 140 g (Fig. 3).

Seminiferous tubule diameter was a good indicator of maturity. Except for two pubertal specimens, all specimens that had a tubule diameter exceeding 108 µm were mature. Only four mature specimens had a smaller tubule diameter (Table 1, Fig. 4).

Color phase was correlated with sexual maturity (Table 2). All but one (0.6 percent, *n* = 165) of the mature specimens were fused. Similarly, 76 percent of the pubertal specimens (*n* = 25) were fused. (The exclusion of speckled and younger specimens will not affect estimates of maturation since only 0.8 percent of speckled specimens (*n* = 520) in the life history sample had testis weights that were equal to or greater than the lowest testis weights for mature (mottled and fused) specimens [Table 2].)

Within each body length group in the life history sample, testes and epididymides were heavier in fused than in mottled specimens (Table 3, Fig. 5). (Neonatal, two-tone and speckled specimens were not plotted because their testis and epididymis weights were much below those of the mottled specimens.) Similarly for the aged sample, when fused and mottled animals within a given body length group were of similar ages, the fused animals had heavier testes and epididymides.

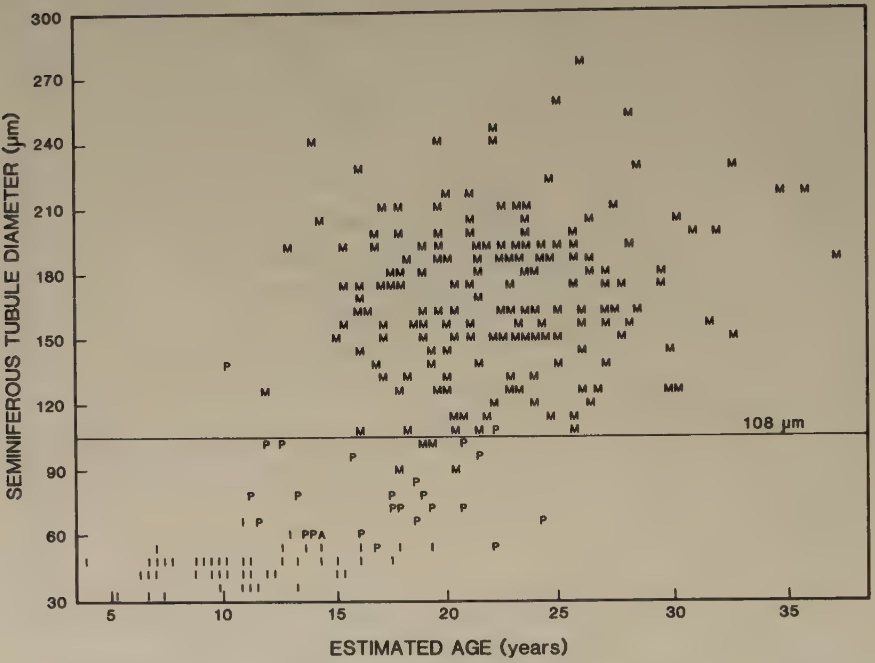

Figure 4. Seminiferous tubule diameter as a function of age; 108 µm is the approximate median seminiferous tubule diameter at attainment of sexual maturity. See Figure 2 for data codes.

Index of Testis Development

The difference between index values for immature, pubertal and mature specimens was significant (ANOVA, $P < 0.0001$, Table 1). The median index value was 0.33 at attainment of puberty and 0.75 at attainment of maturity.

For fused males from the northern offshore stock, the testis index was distributed bimodally (Fig. 6). (This was not the case for testis weight data.) The first peak, from 0.01 to 0.3, corresponds to immature males and the second peak (mode at 1.6) corresponds to mature males. Data for spotted dolphins from the southern stock showed nearly the same pattern.

Mean index values (Table 3) were significantly different among specimens in the five color phases (ANOVA, $P < 0.001$). The mean index value for mottled specimens (0.35) was close to the median index value at attainment of puberty (0.33).

Age at Sexual Maturation

The mean age at attainment of sexual maturity (ASM) for specimens in the histology sample was 13.2 yr (SE = 0.30) based on one reader's estimates and 16.3 yr (SE = 0.44) based on the other reader's estimates ($\bar{x}$ = 14.7). The maturation ogives for these age estimates are shown in Figure 7. The readers'

Table 2. Number of immature, pubertal and mature mottled and fused specimens from the random histology sample.

Color phase	Number immature	Number pubertal	Number mature
Mottled	40	6	1
Fused	14	19	165

differences in estimates are large and partly reflect imprecision in age estimation (Reilly *et al.* 1983). The mean ASM from the average of the two readers' estimates from the aged sample were 16.8 (1973), 15.8 (1974), 14.8 (1976), 16.2 (1977) and 16.2 (1978). (The 1975 sample was too small to allow meaningful analysis.) These estimates show no trend (linear regression, $P = 0.70$).

The mean body length at attainment of sexual maturity based on the histology sample was 186.4 cm for all years combined. For the larger life history sample from 1974 to 1982, the mean lengths at attainment of sexual maturity (index values ≥ 0.75) were 185.5, 187.5, 185.8, 188.6, 186.0, 188.8, 186.7, 191.0 and 192.0 cm, respectively. The increase in mean length at sexual maturity during those years was marginally significant (linear regression, $P = 0.063$).

Seasonality

Mean testis and epididymis weights (Fig. 8) and index values (Fig. 9) for fused specimens (life history sample) showed peaks in July through August and in April. Differences among months were significant (ANOVA, $P = 0.001$ for testis and epididymis weights and $P = 0.0035$ for index values). Similar patterns existed for the southern stock for months for which data were available (no specimens were collected in July or August) (Figs. 8 and 9). Since the relationship between weights of the right testis with and without epididymis is nearly linear (Fig. 10), presence or absence of the epididymis made no difference in the trends.

Seasonal changes in testis histology were also evident. Changes in mean tubule diameter of mature specimens followed a seasonal pattern almost iden-

Table 3. Mean testis weight and index of testis development values by color phase in *S. attenuata* (northern offshore stock).

Color phase	Right-testis weight (g)			Index of testis development		
	Mean	SE	*n*	Mean	SE	*n*
Neonatal	2.4	0.2	56	0.06	0.002	55
Two-tone	6.3	0.2	404	0.10	0.003	403
Speckled	15.0	2.2	520	0.16	0.009	524
Mottled	60.1	5.9	501	0.35	0.022	499
Fused	388.8	6.8	1,564	1.55	0.022	1,566

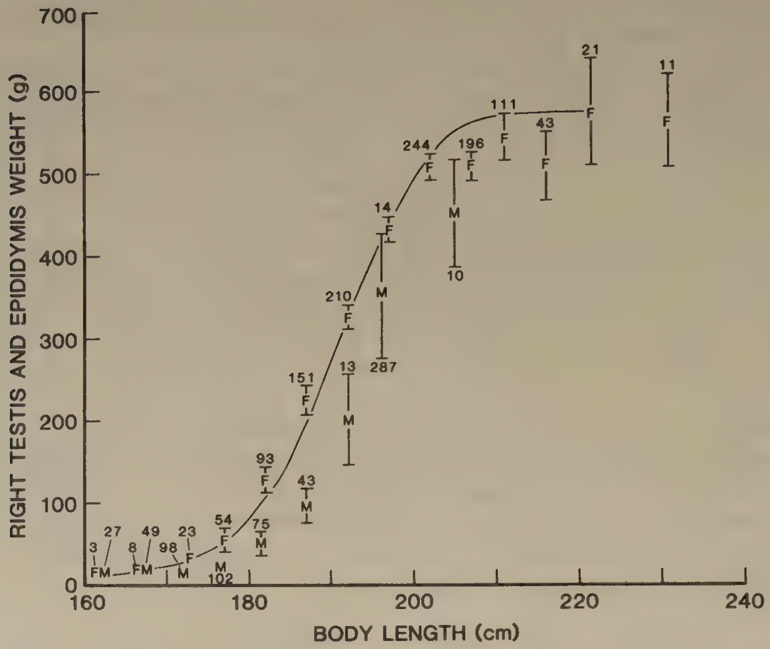

Figure 5. Mean testis + epididymis weight as a function of mean specimen body length in 5-cm length intervals for mottled ($n = 431$) and fused ($n = 1{,}455$) specimens. A three-parameter sigmoid curve is fitted to the data for fused specimens. Error bars represent one standard error from the mean. The sample sizes are given above or below the error bars. M = mottled, F = fused.

tical to that of the testis and epididymis weights and index values (Fig. 11). Monthly differences were significant (ANOVA, $P = 0.0325$). There was also a seasonal pattern in number of specimens that had relatively large quantities of spermatids and spermatozoa (Fig. 12); the number of specimens with spermatids peaked in April, and the number of specimens with spermatozoa peaked in May. The mean diameter of the lumen was greatest in April. There were also peaks of specimens with spermatids and spermatozoa in January and, although spermatozoa levels declined rapidly from May to August, spermatids were observed in most mature specimens throughout the year. We saw no evidence of full recrudescence.

DISCUSSION

Sexual Maturity

Relatively few estimates of the age at attainment of sexual maturity have been made for dolphins based on histological examination of testes. In most of the studies, specimens were considered to be sexually mature if spermatozoa were found in the testes or epididymides (Sergeant 1962, Sergeant *et al.* 1973, Kasuya *et al.* 1974, Kasuya 1976, Perrin *et al.* 1976, Perrin *et al.* 1977,

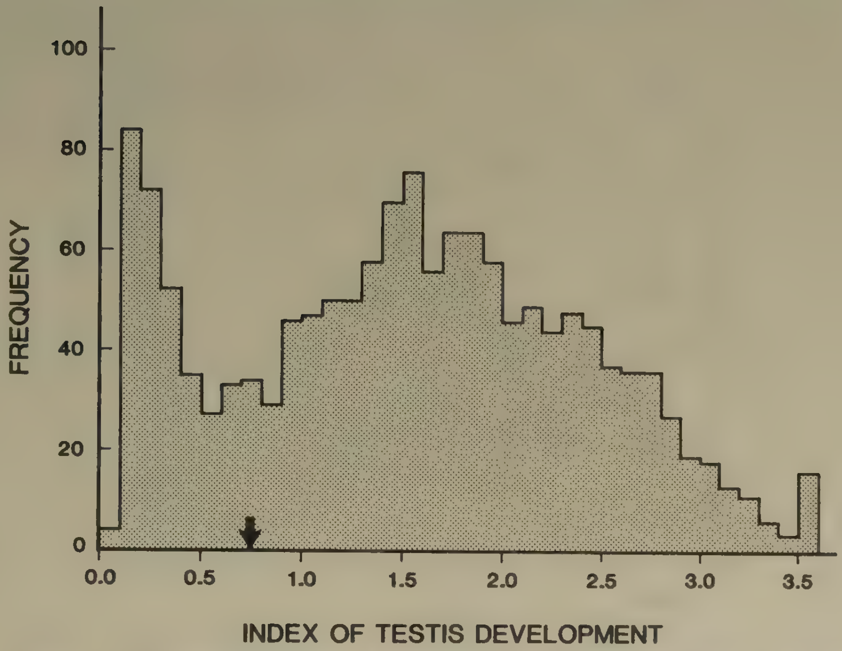

Figure 6. Frequency distribution of the index of testis development (testis + epididymis weight [g] divided by testis length [mm]) for fused specimens ($n = 461$). The arrow marks the median index value at the attainment of sexual maturity.

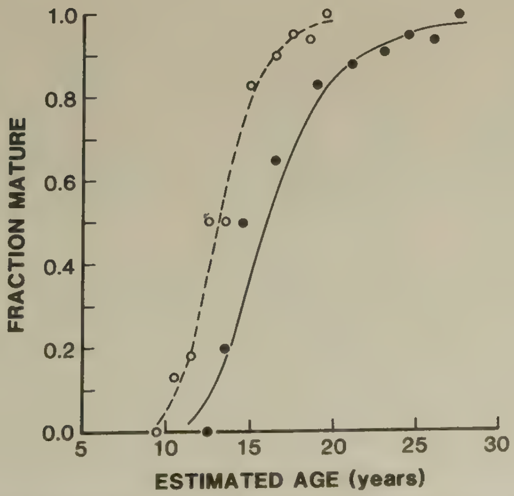

Figure 7. Sigmoid curves fitted to the fraction of sexually mature specimens within each age class based on estimates by each of two readers.

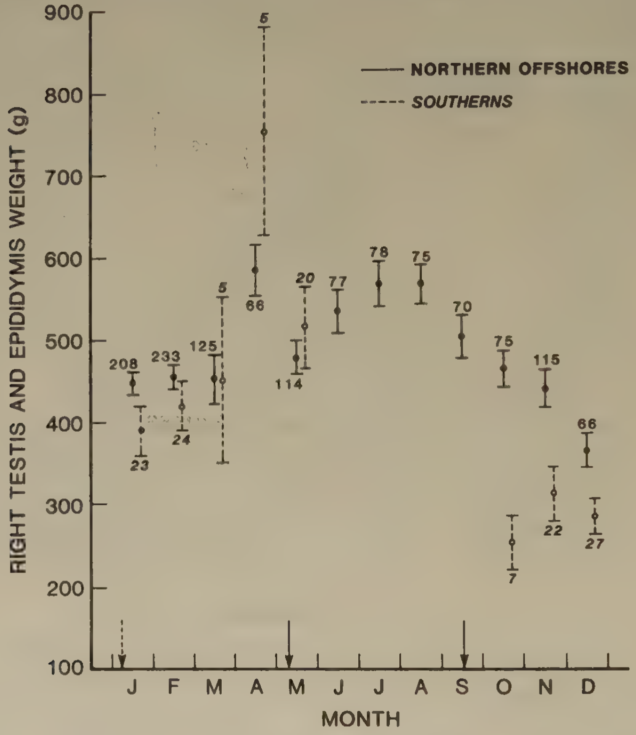

Figure 8. Monthly mean testis + epididymis weight for fused specimens from the northern and southern offshore stocks. Sample sizes are above or below the error bars, which represent one standard error from the mean. The arrows mark the predicted birth dates of the primary calving periods.

Collet and Saint Girons 1984). Sergeant (1962) also considered long-finned pilot whales to be "functionally" mature if the epididymides contained seminal fluid. The state of "pubertal" (also called prepubescent or maturing) has been distinguished from "mature" and "immature" by the presence of spermatogonia and spermatocytes but the absence of spermatozoa (Hirose and Nishiwaki 1971) and relatively narrow seminiferous tubules (Collet and Saint Girons 1984).

Information gained from examination of testes has been used to estimate age, body length and testis weight at maturation in several delphinids (*see* Perrin and Reilly 1984). Estimates of age at maturation for these studies are: *Delphinus delphis*, 6 yr (Collet and Saint Girons 1984); *S. coeruleoalba*, 9 and 8.7 yr (Kasuya 1976, Miyazaki 1977); *S. attenuata*, 11.8 yr (Kasuya 1976) and 12 "layers" (most likely estimate of 11 yr) (Perrin *et al.* 1976); *S. longirostris*, 8.5 to 11.5 yr (Perrin *et al.* 1977); *Tursiops truncatus*, 12 yr (Sergeant *et al.* 1973); and *Globicephala melaena*, 12 yr (Sergeant 1962). It appears that sexual maturity in males is attained at a greater age in spotted dolphins than in many other pelagic dolphins.

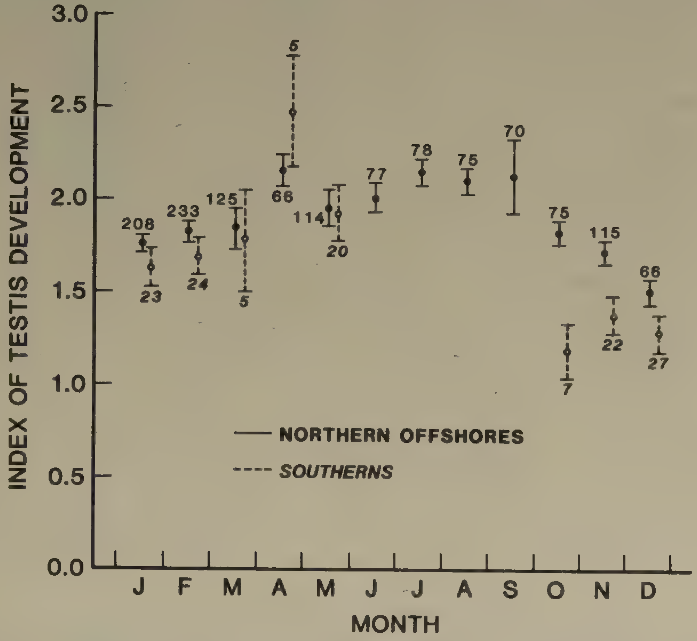

Figure 9. Monthly mean index of testis development for fused specimens from the northern and southern offshore stocks. Sample sizes are above or below the error bars, which represent one standard error from the mean.

Our estimate is higher than that determined for spotted dolphins in the western Pacific. This may reflect real population differences or differences in age determination techniques (*see* Kimura 1980). The methods used to calculate age at attainment of sexual maturity varied greatly, however, for all the species. For example, Kasuya *et al.* (1974), Kasuya (1976) and Miyazaki (1977) estimated median age (and length) at attainment of sexual maturation as that age (and length) at which 50 percent of the specimens were predicted to be mature based on a least-squares linear regression of the proportion of mature specimens within each age (and length) class. Perrin *et al.* (1976) determined that sexual maturation, as indicated by a rapid increase in the diameter of the seminiferous tubules and increase in testis and epididymis weight, is attained at about 10–14 dentinal growth layers (GLGs) and, therefore, the "average" age at sexual maturation is approximately the midpoint of this range. The "average" length of maturation was estimated as the average length of males with 12 GLGs. A similar method was used by Perrin *et al.* (1977) for the spinner dolphin; they determined that spermatogenesis is histologically evident in 50 percent of testes and epididymides that together weighed 94 g. This weight was reached, on "average," at about 9 GLGs, and the average length of specimens with 9 GLGs was 170 cm. Sergeant (1962) first estimated the "mean" body length (16 ft) of functional maturity in the pilot whale as the midpoint between the smallest functionally mature and largest immature spec-

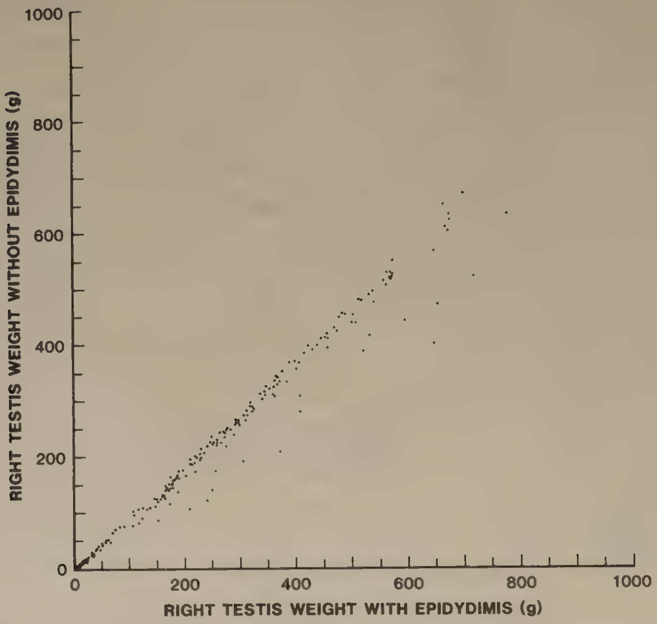

Figure 10. Relation between testis weights with and without epididymis. Each point represents one specimen.

imens. The age at maturation was then estimated to be the estimated age of the mature 16-ft male in the sample. He specified that this estimate of age at maturation would be minimal because of dentinal occlusion. Collet and Saint Girons (1984) used a method for the common dolphin similar to that of Sergeant (1962). Sergeant *et al.* (1973) gave age and length of maturation in bottlenose dolphins, but did not specify how they were obtained. These disparities in the methods used to estimate age at sexual maturation are considerable and indicate that caution must be used in comparing the estimates (*see* also DeMaster 1984).

Laws (1956*b*) found that for 12 species of pinnipeds, 5 species of odontocetes and 5 species of mysticetes, females reach sexual maturity at about 85 percent of asymptotic length (81 percent for (mostly) large odontocetes, 88 percent for mysticetes and 87 percent for pinnipeds). Bryden (1972) added 5 species of pinnipeds, 2 species of odontocetes, and 2 species of mysticetes to this list. Laws (1962) suggested that the mean age of maturation in fin whales in the Antarctic had declined during 1945 to 1956, but that mean length at sexual maturation had not changed. Lockyer (1972) also found a decrease in average age at maturation even though the average length had not changed. Cooke and de la Mare (1983) suggested, however, that these changes were due to sampling bias and not to actual changes in age at attainment of sexual maturity. In contrast, the results of the present study show an increasing length at maturation with time, with no change in the age at maturation. Barlow (1985) also found that

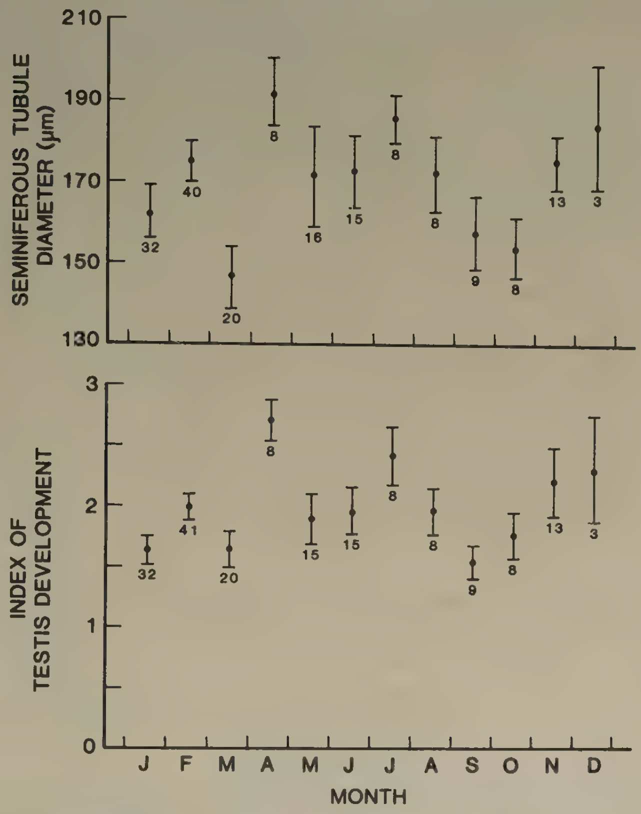

Figure 11. Monthly mean seminiferous tubule diameter and index of testis development values for mature specimens. Sample sizes are below the error bars, which represent one standard error from the mean.

the median length at sexual maturation in female spotted dolphins in the same population had increased between 1974 and 1983. There was no concomitant change in age at maturation for the females (Myrick *et al.*, in press).

It is necessary to have comparable estimates of age and length at maturation in dolphins to make inter- or intra-specific comparisons. We suggest use of the mean age and length estimates (as defined by Cooke) because it is a minimum variance estimator, is easy to compute, does not require a large sample size and provides a variance estimate.

The age at attainment of sexual maturity is higher in males ($\bar{x}$ = 14.7 yr) than in females ($\bar{x}$ = 11.9 yr, Myrick *et al.*, in press) in this population. This difference has also been observed for other dolphins (Sergeant 1962, Kasuya 1976, Perrin *et al.* 1977).

The estimated age (or length) at sexual maturation in our study may be biased by several factors. Age estimates are imprecise, and this imprecision tends to increase with the age of animals (Reilly *et al.* 1983). The age distribution of our sample was not representative of the population; juvenile age classes were

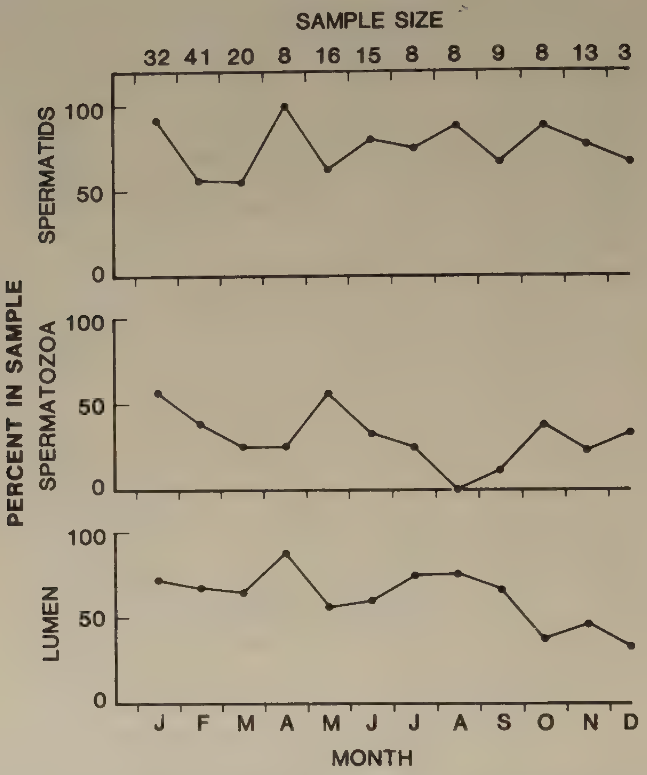

Figure 12. Monthly trends in relative quantities of spermatids, spermatozoa and lumen diameter. The points represent the percentage of mature specimens with most or all of the seminiferous tubules containing spermatids or spermatozoa, and the percentage of specimens with large lumens each month.

underrepresented (Hohn and Scott 1983). If mature animals are more likely to be sampled, the age at sexual maturation would be underestimated. However, the estimates could be overestimates due to a sampling bias caused by segregation of sexually mature, but not yet socially mature, specimens from the main schools (Hohn and Scott 1983).

The results showing correlation of color phase to maturity are comparable to those described by Perrin (1969) and Kasuya *et al.* (1974)—nearly all fused specimens were mature or pubertal and relatively few specimens of other color phases were mature. The development of the fused color phase may be influenced by reproductive hormones, a possibility suggested by Kasuya *et al.* (1974). Color phase may be used to estimate the proportion of sexually mature animals in a sample of spotted dolphins when testis data are not available.

The proportion of mature specimens in the mottled and fused color phases differs for males and females. In females, 96 percent of the fused and 50 percent of the mottled animals are mature (Myrick *et al.*, in press), whereas male mottled specimens are only rarely sexually mature. In addition, the median age of fused females (12.7 yr) and mottled females (9.5 yr) was less than that of males (fused = 14.8 yr, mottled = 10.5 yr).

A nonhistological method for determining sexual maturity in males would be useful. Collet and Saint Girons (1984) used a relation between weight (in g) and length (in cm) of testes (excluding epididymides) to distinguish between states of sexual maturity. They found, from histological analyses of a small sample ($n = 26$), that the ratio of summed right and left testes lengths to summed testes weights (the inverse of the relationship we described) was correlated with state of maturity, where a ratio of about 1.0 identified immature animals. The ratio for mature specimens was 0.2 or less. Index values from Collet and Saint Girons (1984) cannot be compared directly with those from the present study because the testis weights in our sample include the epididymis. But using the mean right-testis length (cm) divided by the mean right-testis and epididymis weight (g) in our study (data from Table 1) gives values of 0.51 for immature, 0.48 for pubertal and 0.05 for mature specimens. Since this sample includes only mottled and fused specimens, the value for immature is lower than for the overall sample of immature specimens (*e.g.*, the mean value for two-tone specimens is 1.0 [Table 2], the same value as immature common dolphins).

Weight of the testis and epididymis can be used as an indicator of sexual maturity within a population. This weight varies greatly, however, between species and stocks, even after considering seasonal differences (*e.g.*, Perrin and Henderson 1984), and thus precludes the use of the weight of testis and epididymis of adults derived from one population to determine maturity in other populations or species. Normalizing testes weight by testes length may provide a more reliable tool for determining sexual state and making inter-specific (or stock) comparisons because it accounts for some of the difference in specimen size, thus allowing for direct comparisons of maturity between species. For example, the spotted dolphins in our study and the common dolphins in the Collet and Saint Girons (1984) study had similar index values for immature and mature even though common dolphins have relatively much heavier testes (Perrin and Reilly 1984). We recommend that future studies investigate the general application of this method to describe maturity and allow for direct inter-stock or inter-specific comparisons of sexual maturity in male dolphins.

Seasonality

Seasonal gonadal changes occur in male dolphins from many populations. Ridgway and Green (1967) suggested a mid- to late-summer breeding season for *Lagenorhynchus obliquidens* and *Delphinus delphis* off central and southern California based on increased testes weights and seminiferous tubule diameters and the occurrence of spermatogenesis. Seasonal changes in testis weights or histological characteristics have also been observed in *S. coeruleoalba* (Hirose and Nishiwaki 1971, Miyazaki 1977), *D. delphis* (Fraser 1953, Gurevich and Stewart 1978, Collet and Saint Girons 1984), *S. attenuata* (Perrin *et al.* 1976) and *S. longirostris* (Perrin and Henderson 1984). Seasonal changes in plasma testosterone were noted in bottlenose dolphins, *Tursiops truncatus,* in the western Atlantic (Harrison and Ridgway 1971) and spinner dolphins, *S. longirostris,* in Hawaii (Wells 1984).

The primary calving seasons for spotted dolphins from the northern offshore stock are May and September (Barlow 1984, Hohn and Hammond 1985). Based on a gestation period of 11.5 months (Perrin *et al.* 1976), mating would have to occur in late May and late September to synchronize with the calving seasons. These mating seasons are within the period of elevated testis weight identified in our study.

For spotted dolphins from the northern offshore stock, however, the seasonal peak for testes weight is midway between the two primary calving seasons (Barlow 1984, Hohn and Hammond 1985). Miyazaki (1977) also found the peak time for male seasonality to be inconsistent with the main breeding season in *S. coeruleoalba* off the coast of Japan. He believed that stock migration and the short sampling season biased his results. Such biases would not be important to our study because of the large sample size and year-round sampling. Best (1969) examined histological sections of sperm whale testes and also found that testicular activity did not increase during the primary female breeding season.

Maximum testis (and epididymis) weight is not a good single indicator of reproductive seasonality for these dolphins. Although peaks in lumen diameter and relative numbers of spermatids coincided with a peak in testes weight in April, the level of spermatozoa was highest in May. The mean testes weight and index of testes development values peaked in July and August, months when spermatid levels and lumen diameters were relatively high but spermatozoa levels were low. For the northern offshore stock, one calving season occurred at about the time when spermatozoa levels were high but testes weights and index values were relatively low (September). In the southern stock, the seasonal distribution of testes weights and index values were similar to those in the northern stock, yet only one calving season (in January) has been identified (Barlow 1984, Hohn and Hammond 1985). On the basis of a limited sample, however, Hohn and Hammond (1985) indicated that a second calving season may occur about six months later. We currently have no explanation of why the testis weight seasonality profile is similar and the calving seasons are different between northern and southern offshore stocks. More data from the southern stock are needed to answer this question. Some calving occurs throughout the year in the northern offshore stock, indicating that at least some males do not maintain the same breeding season or they are reproductive throughout the year.

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Hammond, F. Hester, T. Kasuya, J. Mead, A. Myrick, W. Perrin, S. Reilly, M. Scott and an anonymous reviewer reviewed the manuscript.

LITERATURE CITED

BARLOW, J. 1984. Reproductive seasonality in pelagic dolphins of the eastern tropical Pacific. Pages 191–198 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

BARLOW, J. 1985. Variability, trends, and biases in reproductive rates of spotted dolphins (*Stenella attenuata*). Fishery Bulletin (U.S.) 83(4).

BEST, P. B. 1969. The sperm whale (*Physeter catodon*) off the west coast of South Africa. 3. Reproduction in the male. Division of Sea Fisheries Investigational Report No. 72. 20 pp.

BLOOM, W., AND D. W. FAWCETT. 1975. A textbook of histology. 10th Edition, W. B. Saunders Co., Philadelphia, Pa. 1,033 pp.

BRYDEN, M. M. 1972. Growth and development of marine mammals. Pages 1–80 *in* R. J. Harrison, ed. Functional anatomy of marine mammals. Volume 1. Academic Press, New York, NY.

CHARNY, C. W., A. S. CONSTON AND D. R. MERANZE. 1952. Testicular developmental histology. Pages 597–608 *in* R. W. Miner, ed. Biology of the testes. Annals of the New York Academy of Sciences 55(4):543–742.

COLLET, A., AND H. SAINT GIRONS. 1984. Preliminary study of the male reproductive cycle in *Delphinus delphis* in the eastern north Atlantic. Pages 355–360 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

COOKE, J. G., AND W. K. DE LA MARE. 1983. The effects of variability in age data on the estimation of biological parameters of minke whales (*Balaenoptera acutorostrata*). Reports of the International Whaling Commission 34:333–338.

DEMASTER, D. P. 1984. Review of techniques used to estimate the average age of sexual maturity in marine mammals. Pages 175–180 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

FRASER, F. C. 1953. Report on Cetacea stranded on the British coasts from 1948 to 1966. British Museum of Natural History. 48 pp.

GUREVICH, V. S., AND B. S. STEWART. 1978. Structure of kill of the common dolphin *Delphinus delphis* from eastern tropical Pacific in 1977. Final report for Contract No. 03-78-M02-0101, Southwest Fisheries Center, La Jolla, California, 19 pp. Available from B. S. Stewart, Hubbs-Sea World Research Institute, San Diego, CA 92109.

HARRISON, R. J., AND S. H. RIDGWAY. 1971. Gonadal activity in some bottlenose dolphins (*Tursiops truncatus*). Journal of Zoology (London) 165:355–366.

HIROSE, K., AND M. NISHIWAKI. 1971. Biological study on the testis of the blue white dolphin, *Stenella caeruleoalba*. Journal of the Mammal Society of Japan 5:91–98.

HOHN, A. A., AND P. S. HAMMOND. 1985. Early postnatal growth of the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fishery Bulletin (U.S.) 83(4).

HOHN, A. A., AND M. D. SCOTT. 1983. Segregation by age in schools of spotted dolphin in the eastern tropical Pacific. Page 47 *in* 5th Biennial Conference on the Biology of Marine Mammals, Boston, MA. (Abstract.)

KASUYA, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Scientific Reports of the Whales Research Institute 28:73–106.

KASUYA, T., N. MIYAZAKI AND W. H. DAWBIN. 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. Scientific Reports of the Whales Research Institute 26:157–226.

KIMURA, M. 1980. Variability in techniques of counting dentinal growth layer groups in a tooth of a known-age dolphin, *Tursiops truncatus*. Pages 161–169 *in* W. F. Perrin and A. C. Myrick, Jr., eds. Age determination of toothed whales and sirenians. Reports of the International Whaling Commission, Special Issue 3.

LAWS, R. M. 1956*a*. The elephant seal (*Mirounga leonina* Linn.) III. The physiology of reproduction. Falkland Islands Dependencies Survey, Scientific Reports No. 15. 65 pp.

LAWS, R. M. 1956*b*. Growth and sexual maturity in aquatic mammals. Nature 178: 193–194.

LAWS, R. M. 1962. Some effects of whaling on the southern stocks of baleen whales. Pages 137–158 *in* E. D. Le Cren and M. W. Holdgate, eds. The exploitation of natural animal populations. Blackwell Scientific, Oxford, UK.

LOCKYER, C. H. 1972. The age of sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug. Journal du Conseil International pour l'Exploration de la Mer 34:276–294.

MIYAZAKI, N. 1977. Growth and reproduction of *Stenella coeruleoalba* of the Pacific coast of Japan. Scientific Reports of the Whales Research Institute 29:21–48.

MYRICK, A. C., JR., A. A. HOHN, J. BARLOW AND P. A. SLOAN. In press. Reproduction of female spotted dolphin, *Stenella attenuata*, from the eastern tropical Pacific. Fishery Bulletin (U.S.).

MYRICK, A. C., JR., A. A. HOHN, P. A. SLOAN, M. KIMURA AND D. D. STANLEY. 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. NOAA-Technical Memorandum-NMFS-SWFC-30. 17 pp.

PERRIN, W. F. 1969. Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* Lonnberg (Cetacea, Delphinidae). Zoologica (New York) 54:135–149.

PERRIN, W. F., J. M. COE AND J. R. ZWEIFEL. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fisheries Bulletin (U.S.) 74(2):229–269.

PERRIN, W. F., AND J. R. HENDERSON. 1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. Pages 417–430 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

PERRIN, W. F., D. B. HOLTS AND R. B. MILLER. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fishery Bulletin (U.S.) 75(4):725–750.

PERRIN, W. F., AND S. B. REILLY. 1984. Reproduction parameters of dolphins and small whales of the Delphinidae. Pages 97–133 *in* W. F. Perrin, *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

PERRIN, W. F., M. D. SCOTT, G. J. WALKER AND V. L. CASS. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA-Technical Report-NMFS-28.

REILLY, S. B., A. A. HOHN AND A. C. MYRICK, JR. 1983. Precision of age determination of northern offshore spotted dolphins. NOAA-Technical Memorandum-NMFS-SWFC-35. 27 pp.

RIDGWAY, S. H., AND R. F. GREEN. 1967. Evidence for a sexual rhythm in male porpoises, *Lagenorhynchus obliquidens* and *Delphinus delphis bairdi*. Norsk Hvalfangst-Tid. 1:1–18.

SERGEANT, D. E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Fisheries Research Board of Canada, Bulletin 132. 84 pp.

SERGEANT, D. E., D. K. CALDWELL AND M. C. CALDWELL. 1973. Age, growth and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. Journal of the Fisheries Research Board of Canada 30:1009–1011.

WELLS, R. S. 1984. Reproductive seasonality and social behavior of Hawaiian spinner dolphins, *Stenella longirostris*. Pages 465–472 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

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A Small Vessel Technique for Tracking Pelagic Fish

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Introduction

The advent of ultrasonic telemetry techniques for monitoring fish movements in the wild has greatly increased our understanding of the behavior and physiological capabilities of pelagic fish (Carey, 1983). The development of pressure sensitive transmitters has allowed insights into the remarkable pressure (depth) and temperature tolerances of these animals while simultaneously revealing their fine-scale horizontal movements.

Previous tracking studies involving pelagic species have been carried out using large fishing or oceanographic research vessels. Because of the high operating costs of these vessels and the heavy demands on their time, comparatively few fish have been tracked. Also, the tracks that have been made come from widely scattered areas. Thus, although valuable data have been acquired from individuals of several species, only rarely have enough replicate tracks been obtained to give a reasonable indication of the normal daily behavior of a species in a particular location. Pelagic species that have been tracked include skipjack tuna, *Euthynnus pelamis* (Yuen, 1970); yellowfin tuna, *Thunnus albacares* (Carey and Olson, 1982); albacore, *T. alalunga* (Laurs et al., 1977); swordfish, *Xiphias gladius* (Carey and Robison, 1981); blue marlin, *Makaira nigricans* (Yuen et al., 1974); mackerel sharks (Carey et al., 1981); and Atlantic salmon, *Salmo salar* (Westerberg, 1982).

This paper reports on the development of a technique for using a small vessel for the ultrasonic tracking of pelagic fish. Our system produces high-resolution data and is sufficiently adaptable and cost-effective to allow prolonged tracking efforts in a variety of situations. Because of its modest cost, a small vessel can be dedicated to a tracking project for extended periods. This permits acquisition of many replicate multi-day tracks. Thus, sufficient amounts of data can be acquired to yield reliable information about the sequential daily behavior of a target species. Details of our system and methods have been included to allow other workers to adapt our techniques to their own needs.

The impetus for development of our tracking technique began when the Honolulu Laboratory of the National Marine Fisheries Service (NMFS) Southwest Fisheries Center pioneered the modern use of fish aggregating devices (FAD's) by deploying several of these buoys in Hawaiian waters in 1975 (Matsumoto et al., 1981). These deep-water FAD's have proved to be very effective and their use has spread throughout the Indo-Pacific (Shomura and Matsumoto, 1982). However, the influences of FAD's on fish behavior which result in the aggregation of pelagic fishes at these buoys are not understood. Given the importance of FAD's, the high costs associated with FAD deployment, and unanswered questions relating to stock harvesting and management, we initiated a project using ultrasonic transmitters and a small pursuit vessel to document the movements of pelagic species associated with FAD's. To date, our efforts have concentrated solely on yellowfin tuna and bigeye tuna, *T. obesus*, with fork lengths between 50 and 75 cm.

Methods

General

Our two major objectives when equipping the vessel were simplicity and redundancy. The data acquisition and recording systems were designed to emphasize shore-side data processing,

ABSTRACT—Tracking of pelagic fish has previously been conducted from large research or fishing vessels, both of which are expensive to operate. We have adapted advances in ultrasonic tracking technology to permit tracking of pelagic fish from a small (33-foot) vessel. Sportfishing techniques have been successfully employed to capture fish for tracking.

The use of a small vessel has many advantages including maneuverability in congested areas, the ability to work both offshore and close to shore, high responsiveness to changes in fish behavior, and low operating costs. Low operating costs allow the vessel to be utilized over extended periods, thereby permitting replication of experiments. High quality data on the vertical and horizontal movements of pelagic fish have been acquired for periods of up to 6 days. These techniques could be utilized to track fish inexpensively in a wide range of locations.

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thereby maximizing the use of on-board space and equipment for actual acquisition and storage of high-quality raw data. Secondary objectives were minimizing operating costs and maximizing crew comfort, thus improving our ability to track fish for long durations.

The Vessel

The R/V *Kaahele'ale* is a 33-foot vessel built for the U.S. Navy as a personnel boat. It was acquired by the NMFS in 1979 and modified for nearshore fisheries research, primarily telemetry. As modified, the vessel has an open-stern deck, a semi-enclosed central cabin with engine beneath, and a fully enclosed forward cabin. The stern deck is equipped for fishing and tagging. The central cabin houses the steering console and an instrument rack containing the telemetry equipment, navigation equipment, and radar. The forward cabin is air conditioned and contains two bunks, a work bench, an expendable bathythermograph (XBT) system, and a microwave oven.

The vessel is powered by a single screw driven by a GM-671[1] diesel engine through an Allison hydraulic transmission. Two 120-gallon fuel tanks are backed with a 50-gallon reserve tank. At cruising speed (11 knots), fuel consumption is 10 gallons/hour, at trolling speed (7.5 knots) it is 5 gallons/hour, and during tracking operations fuel consumption is usually less than 3 gallons/hour. The main engine alternator supplies a 24 volt main battery which powers the starter motor, the radar, and autopilot. Radios, tracking instrumentation, navigation lights, and fathometers are powered by a separate 12V DC battery bank. A 7.5 KW 120V AC diesel generator (Onan) is housed below a portion of the stern deck and powers the XBT system, the microwave oven, the forward cabin air conditioner, and an automatic 12V battery charger.

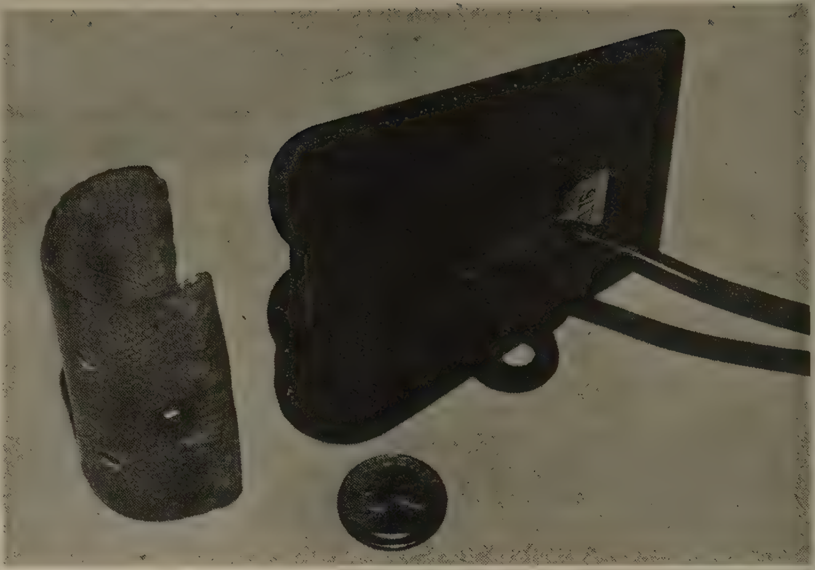

Figure 1.—The directional hydrophone is shown with fiberglass faring removed. Holes in the faring permit attachment to hydrophone body and allow water to flood the space between the hydrophone and the faring. The hydrophone sideplate has been removed to show hydrophone and preamplifier.

Tracking Apparatus

Transmitters

Pressure sensitive 50 KHz ultrasound transmitters were purchased from Vemco, Halifax, Nova Scotia. Two types of transmitters have been used, one with an expected operation life of up to 22 days and the other with nominal expected life of 3 days. We have found maximum open ocean operating ranges to be about 0.8 miles for the 3-day tags, and about 0.5 miles for the 22-day tags. The transmitters are pressure sensitive such that the pulse frequency of the 50 KHz carrier signal is directly proportional to increasing pressure (depth). Normal operating range is zero (surface) to 500 psi (370 m depth). The 22-day duration transmitters are cylindrical (8.0 cm long and 1.6 cm diameter) and weigh 27.7 g in air and 11.7 g in seawater. The 3-day duration transmitters are of similar specifications. The transmitters are equipped with magnetically operated reed switches for rapid activation and have a nylon loop at one end for use in attachment to the fish (discussed later).

Receivers

The 12V DC amplifier/receivers (CR-40, CAI Co.) are matched to the transmitters with 50 KHz crystal-controlled oscillators. These receivers amplify and convert the telemetered pulses into an audible signal. Two receivers were installed on the vessel in case one of the units failed during a track.

Hydrophone

The directional hydrophones were also manufactured by Vemco. However, a small but very significant modification was made after delivery from the factory. This modification involved the fabrication and installation of a 2 mm thick fiberglass faring over the leading face of the hydrophone (Fig. 1). This faring serves to protect the actual sensor from physical damage and, more importantly, reduces noise generated by water passing over the hydrophone. The signal/noise ratio is improved to such an extent that usable data can be acquired at boat speeds in excess of 7 knots. We can therefore track and acquire depth data from fast moving fish. The faring also allows the boat to be driven at 11 knots without damage to the hydrophone. No reduction in operating range

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[1] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

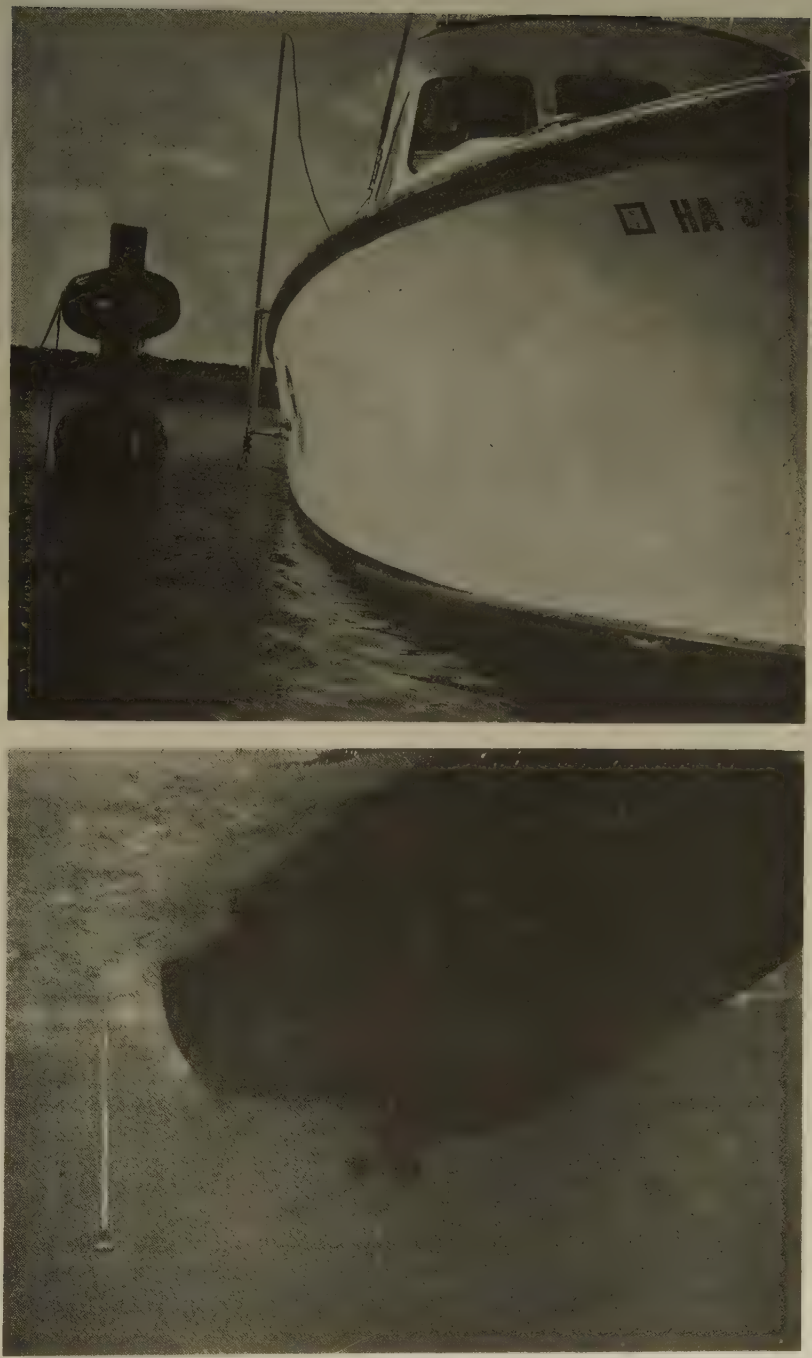

Figure 2.—Hydrophone Mounting. Top: The tracking hydrophone is in retracted position. Two triangular aluminum brackets mounted above the waterline allow the hydrophone to be lifted out of the water when not in use. Bottom: The hydrophone mounting pole is lowered through the support brackets to a position in which the hydrophone is clear of the keel and is unaffected by turbulence from the boat hull.

was observed following installation of the faring.

The hydrophone is braced within a stainless steel bracket bolted to the end of a 10-foot length of 1-inch I.D. galvanized pipe. The shielded cable from the hydrophone to the amplifier is threaded through the pipe. Shielding the cable is necessary to reduce radio frequency interference.

The hydrophone mounting pipe is deployed amidships using two triangular brackets, constructed of 1-inch I.D. aluminum tubing, which are bolted, one above the other, through the hull above the waterline. The pole is free to slide through the brackets and is held in place by thumbscrews. Thus, the hydrophone can be lowered for tracking and raised out of the water when not in use. This outrigger type of mounting allows the hydrophone to run about 5 feet below the surface and 6 feet to the side of the keel where it is unaffected by water turbulence generated by the hull (Fig. 2). During tracking, the hydrophone is secured facing forward in parallel with the keel of the boat, and localizing the transmitter (i.e., the fish) is accomplished by turning the vessel.

Depth Data Logging

A data processor/frequency counter (Telonics, TDP-2) is connected to the audio output of the receiver. This processor unit provides a digital display of the inter-pulse interval which is recorded manually at regular intervals and which gives an immediate indication of the fish depth and any changes in behavior. A cassette tape recorder is also connected to the audio output of the receiver. This provides a continuous record of the telemetered depth data for fine-scale plotting and analysis ashore.

Navigation

Three types of fixes are used to determine the vessel's position during tracking. The primary navigational reference is by Loran C (Furuno LC-80). This unit provides latitude and longitude in-

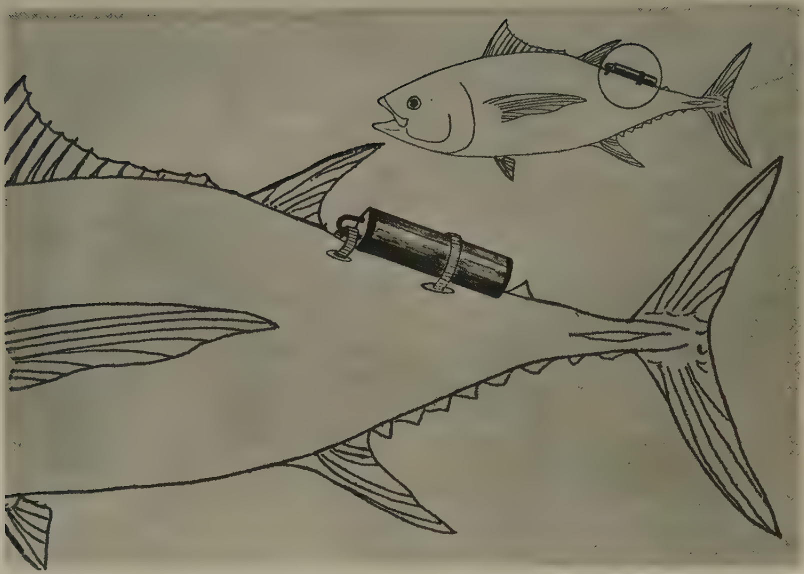

Figure 3.—The ultrasonic transmitter is attached to the dorsal surface using two nylon tiewraps inserted through the dorsal musculature and pterygiophores.

formation and also the vessel's course and speed. These latter data are useful in subsequent onshore analysis of the fine-scale movements of the fish. The waypoint storage capability of this unit also permits instantaneous information about the vessel's current position relative to starting or other important (e.g. FAD) positions. Supplementary visual fixes on charted landmarks are made using a hand-bearing compass or sextant. These visual fixes are made hourly to ensure the accuracy of the Loran C positions. The 24V DC radar unit is used to acquire accurate distances to landmarks or FAD's.

Oceanographic Information

Knowledge of the thermal structure of the ocean is essential to interpretation of the movements of the fish. Temperature data are acquired using a 110V AC expendable bathythermograph (XBT) system (Sippicon, Mass.). The XBT probes are deployed about every 3 hours or whenever the fish being followed moves into new waters (e.g., onshore to offshore). A bucket thermometer is used to verify the accuracy of the XBT surface temperatures.

Water current direction at FAD locations is determined by visual inspection of plastic streamers attached to the FAD's mooring chain. When operating in inshore areas (<100 fathoms) a fathometer is used to record ocean depth and to assist in determining geographic position.

Fishing and Tagging Techniques

The research vessel is equipped for both handline (drift) fishing and trolling. To date, most fish have been caught trolling. Artificial trolling lures tailored to the size of the target species are used with single ''J''-type hooks. Large reels (14/0, Penn Reels, Pennsylvania) and 130-pound test line are used so that the fish can be reeled in rapidly to reduce capture stress. The reels are set with very light drag to reduce injury to the fish's mouth. After the initial strike and run, the drags are tightened and the fish brought to the boat as quickly as possible. Occasionally, the fish are towed behind the slowly moving vessel while the remaining fishing gear is retrieved and the stern deck prepared for tagging.

The tagging cradle is located in the center of the transom. The cradle is a foam-lined, ''V''-shaped trough with one side hinged to allow variable gape to accommodate fish of different sizes. The fish to be tagged is lifted aboard, lightly wedged into the cradle and its eyes covered with a wet chamois cloth. These procedures are usually sufficient to immobilize the fish. Once aboard, species identification is verified, the hook removed, and mouth damage assessed and the fish length measured. Handling is performed without gloves which remove large amounts of mucus from the fish's surface.

Using the nylon loop embedded in one end of each transmitter, the unit is attached to the dorsal surface of the fish (adjacent to the second dorsal fin) using nylon "tie-wraps." These are inserted through the dorsal pterygiophores using sharpened hollow brass needles. Two tiewraps are used per fish; one passing through the transmitter loop, the other half way along the transmitter's length to prevent the transmitter from wobbling from side to side. After insertion through the musculature, the tie-wraps are cinched down and trimmed (Fig. 3). The fish is then released. The entire operation requires the fish to be on board between 1 and 2 minutes.

Tracking Techniques

Testing of the transmitter/receiver system has demonstrated that maximum operational range is between 0.25 and 0.8 n.mi., depending on the type of transmitter being used. Furthermore, we have established that maximum deflection of the signal amplitude meter on the CAI receiver occurs when the transmitter is within about 200 m of the vessel. Consequently, during tracking we attempt to keep the fish at just the distance where maximum gauge deflection occurs. This gives us added confidence in the accuracy of our tracks and also that we are not unduly "crowding" the fish. The directional hydrophone (and therefore the boat) is kept pointed at the fish by maximizing the audio output of the receiver. The small size of the vessel permits rapid changes of direction and rapid identification of the direction of the signal. Due to the noise reduction resulting from the installation of the hydrophone faring, a fish can be pursued at up to 7 knots if it appears to be drawing away. At higher pursuit speeds depth data recording must be temporarily suspended because the noise of water rushing past the hydrophone masks the transmitter's signal.

Data Acquisition

During tracking, four types of data are acquired: 1) A continuous tape of fish-depth data from the audio output of the CAI receiver, 2) water depth/temperature profiles (XBT), 3) water depth, and 4) navigational data. Navigational data are recorded every 10 minutes and include: 1) Time, 2) heading/engine RPM, 3) Loran C fixes, and 4) visual and radar fixes (usually taken hourly). When close enough to a FAD, its range and bearing from the vessel are also recorded every 10 minutes. A narrative commentary is compiled to assist in subsequent data analysis.

Data Analysis

Vertical Data

Figure 4 summarizes the system for acquisition and analysis of vertical movement data. Once ashore, the recorded information is played from the cassettes into a Telonics TDP2 Data Processor. This processor is modified to output a +5V DC square wave each time a sound pulse is detected. A Hewlett Packard (HP) frequency counter (HP5308A) is used to time every other pulse interval. An HP 9845 computer with real-time clock converts the pulse intervals to depth and plots a graph of depth versus elapsed time. This original hard copy of the fish's swimming depth contains some erroneous points which are eliminated by tracing the depth-time profile on an Apple computer digitizer pad. This "cleaned" track (where depth is plotted every 10 seconds) is then stored on floppy disks prior to final plotting and analysis. Bathythermograph temperature profiles are superimposed on the final printouts (Fig. 5).

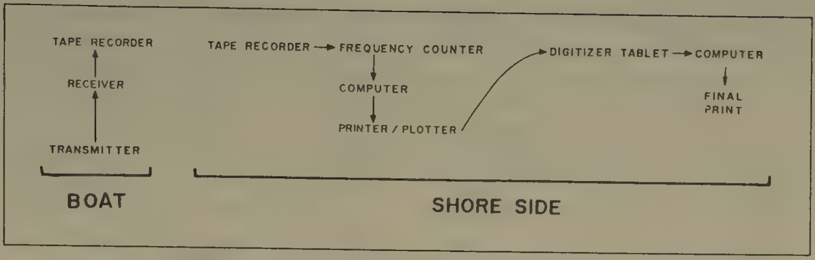

Figure 4.—Schematic representation of the data acquisition and analysis process.

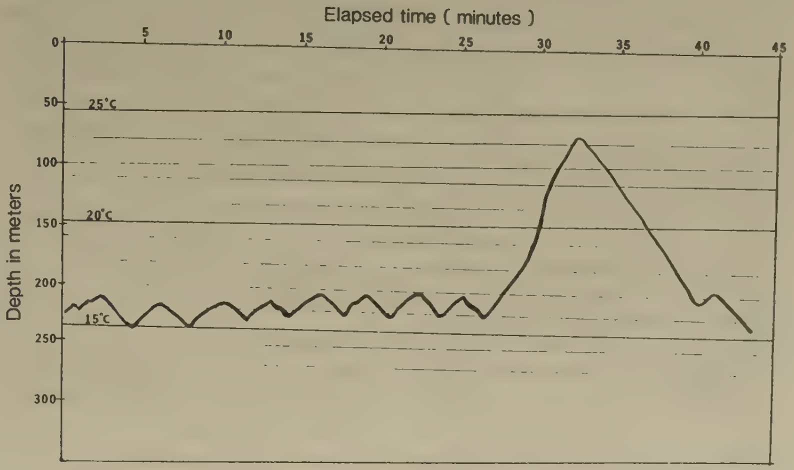

Figure 5.—A 45-minute vertical movement plot. Continuous recording of vertical movement data on cassette tapes allows both fine-scale and large phenomena to be discerned. Superimposing XBT data indicates that the swimming depth of this bigeye tuna is strongly influenced by the 15° and 17° C isotherms. Depth data of this type are recorded for the entire duration of each track.

Horizontal (Position) Plotting

Because of the proximity of the tracking vessel to the target fish, no attempt is made to distinguish between the positions of the two. Plots are made on navigation and bathymetry charts based on Loran Č positions recorded manually at sea. These relative positions are checked against the visual and radar fixes that were concurrently collected. Where applicable, fathometer readings are used as cross references for the other navigational data. Fine-scale movements of fish in the immediate vicinity of FAD's are plotted using manual records of the buoy's range and distance relative to the vessel.

Results

Since the installation of the tracking equipment in its current form, we have acquired 11 tracks of yellowfin tuna and 2 tracks of bigeye tuna that were caught near FAD's or near the adjacent coastline. The duration of the tracks ranged from 8 hours to 6 days.

All but one of the fish was caught by trolling. The small (6/0) size of hooks and light drag settings result in comparatively minor hook wounds. In only one instance has a fish died immediately upon release. All others have shown rapid recoveries to, what we believe, based on consistency within and across samples, is normal behavior. None of these tracks have been terminated due

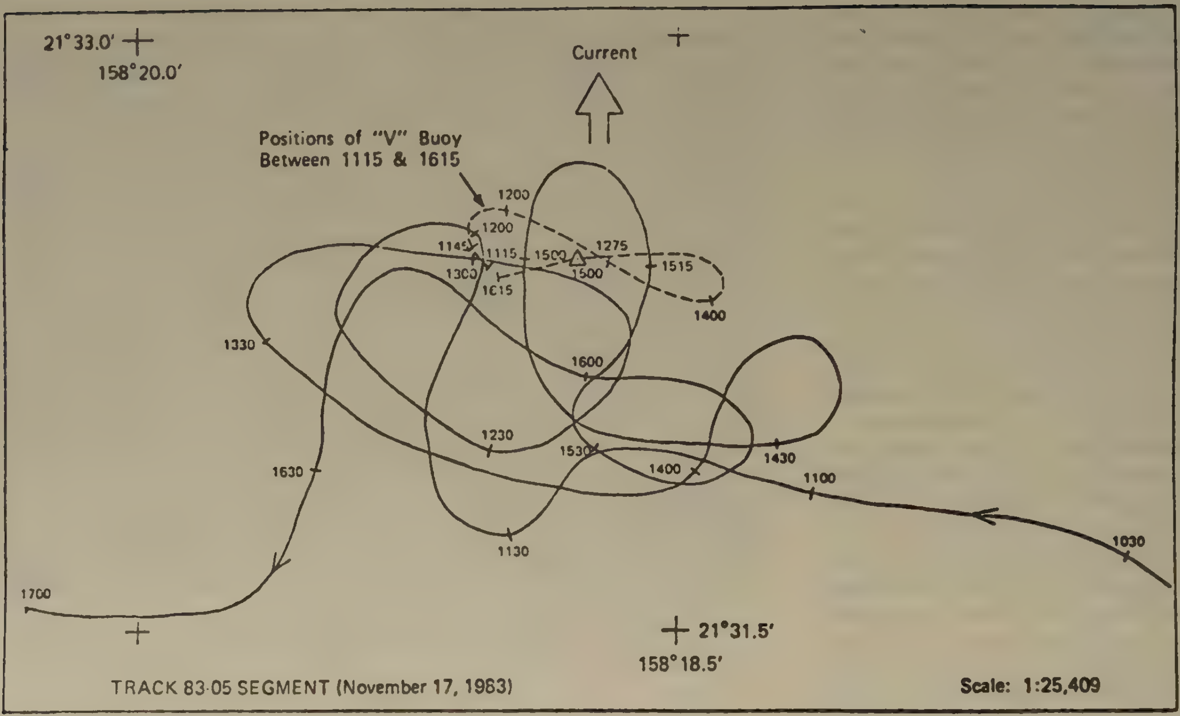

Figure 6.—Fine-scale horizontal plotting. Loran C, radar, and visual fixes allow fine-scale movements to be plotted. After arriving at FAD "V" off of Waianae, Oahu, this 55 cm yellowfin tuna spent about 85 percent of the next 5 hours on the upcurrent side of the buoy. The "Figure 8" movement of the buoy can also be plotted.

to death of the fish.

Captive fish tagged with the "double tie-wrap" method and observed in large tanks at the Kewalo Research Facility of the NMFS Honolulu Laboratory were able to swim normally with the school and appeared healthy after the 2-week observation period ended. In addition, a fortuitous recovery of a tagged fish by a fisherman attests to the suitability of our trolling/tagging technique. This fish was caught by a fisherman trolling near a FAD 3 weeks after we obtained a 36 hour track of it.

Discussion

Although almost all of the technology incorporated in the current research had been previously developed and utilized by others, we feel we have made significant advances in successfully adapting these techniques to a small vessel. Also, the ability to chase pelagic, highly mobile fish at 7 knots in the open ocean and still simultaneously collect vertical movement data is an innovation. We believe that our cassette recording and subsequent plotting of the vertical movement data has produced higher resolution vertical movement data than have previously been published. The continuous depth record has revealed phenomena (such as rapid vertical excursions and small scale oscillations) that manually collected data would have missed (Fig. 5). When the XBT data are superimposed on the tracks, much of the vertical behavior shows correlations with temperature (Fig. 5). Similar temperature influenced behaviors have been observed in bluefin tuna, *Thunnus thynnus* (Carey and Olsen, 1982).

The Loran C system of geographic plotting, when referenced with visual fixes, provides high resolution positioning of both large- and small-scale movements (Fig. 6). When Loran information is used in conjunction with visual fixes and radar ranges, small-scale movements of both the fish and FAD's can be plotted. Knowledge of the relationship between signal amplitude and transmitter distance lends confidence to the precision of the small-scale plots.

The small size of the tracking vessel has proved to have several advantages. For example, while able to pursue fish in the open ocean, the maneuverability of the vessel has also permitted unobtrusive data collection even when in the midst of many other vessels fishing at the FAD locations. Also, fish have been tracked to within 200 m of shore where larger vessels could not safely go. Similar situations occur in other locations such as straits, bays, lakes, and estuaries where tracking studies might be worthwhile but where large vessels would be too cumbersome. A vessel such as ours is capable of continuously following a fish both when it is moving in inshore (e.g., estuarine) waters and also when it moves offshore where it would be beyond the range of fixed hydrophone arrays or of very small vessels such as skiffs.

Of course, small vessels are not suitable for mid-ocean work or offshore locations beyond refueling range. However, they could be used very successfully in association with a larger mother ship which could be performing other tasks while the small pursuit vessel was tracking.

The comparatively low hydrodynamic and mechanical noise generated by our small hull allowed the hydrophone to be attached directly to the side of the boat, thereby precluding the need for complex towed arrays such as have been deployed in some other tracking studies which used large vessels. Similarly, because a small vessel is very maneuverable and can accelerate quickly, the hydrophone can be permanently locked in an orientation parallel with the keel and the entire boat turned to accomplish maintaining contact with the target fish. This high responsiveness eliminates the need for rotatable or multi-head hydrophone systems such as have sometimes been used in the past.

Much of our tracking work has been conducted out of small boat harbors with depths of 2 fathoms or less and which would have been inaccessible to larger fishery research vessels. Each 24 hours of tracking consumes about 70 gallons of fuel. At this rate our vessel can track for at least 3 days without refueling, which can be conducted at any nearby small boat harbor. We have found crews of three sufficient for all phases of the field work. This, combined with the low fuel costs, makes the total operating cost of each tracking expedition extremely modest when compared with the $5,000 to $15,000 daily costs of large research vessels or commercial fishing boats. Our modest expenses enable the vessel to be dedicated to the tracking project for extended periods. This allows replicate tracks of different species from various locations. Also, because the vessel is committed to the tracking project full time, we can take advantage of short term increases in fish abundance and avoid fishing when fish are not abundant. Our ability to use sport fishing techniques to obtain fish for tracking indicates that labor-intensive trapping methods or expensive bait-boat techniques are not obligatory for a successful tracking program.

The small size and modular nature of the actual tracking equipment is such that it could be quickly installed on almost any suitable vessel. The major installation requirement is the bracing of the hydrophone brackets to the hull. However, since the bracket mountings are well above the water line, even this aspect of the installation could easily be repaired when the tracking is completed. The availability of an AC power generator has proved to be essential. Not only does this provide XBT capabilities but also allows improvement in crew facilities such as hot food and air conditioning.

The two major limitations of our system are fuel capacity and crew fatigue. We have solved the former by refuelling during prolonged tracks. However, this technique may be unique to our project because of the proximity of small boat harbors and the rhythmicity of behavior of some of our fish which has allowed us to relocate them after temporary suspension of tracking. Crew fatigue is inevitable with a small vessel after a few days on water. We feel that in our case this could be substantially remedied by using only a slightly larger vessel (e.g., 40-45 ft) which would be somewhat more spacious and comfortable and yet which would retain the desirable characteristics of maneuverability and low operating costs. Another possible technique would be the use of a shuttle vessel to exchange crews on the pursuit vessel.

We are currently unable to be completely sure whether or not the fish being tracked is travelling alone or in a school. We feel this shortcoming will be rectified by the installation of a chromoscopic fish finder.

In general terms, however, we feel that we have developed a cost-effective technique for acquiring high-quality tracking data which could be adapted to a range of small vessels operating in a variety of situations and locations. This, in turn, will result in a significant increase in our understanding of the normal behavior of commercially important fish species about which not much is currently known. Such an increase in our understanding will improve both management and fishing techniques.

Literature Cited

Carey, F. G. 1983. Experiments with free swimming fish, p. 57-68. *In* P. G. Brewer (editor), Oceanography, the present and the future. Springer-Verlag, N.Y.

Carey, F. G., J. M. Teal, and J. W. Kanwisher. 1981. Visceral temperatures of mackerel sharks. Physiol. Zool. 54:334-344.

Carey, F. G., and R. J. Olson. 1982. Sonic tracking experiments with tunas. Coll. Vol. Sci. Papers Int. Comm. Cons. Atlantic Tuna 17(2): 458-466.

Carey, F. G., and B. H. Robison. 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fish. Bull. (U.S.) 74(2):277-292.

Laurs, R. M., H. S. H. Yuen, and J. H. Johnson. 1977. Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. Fish. Bull. 75(2):347-355.

Matsumoto, W. M., T. K. Kazama, and D. C. Aasted. 1981. Anchored fish aggregating devices in Hawaiian waters. Mar. Fish. Rev. 43(9):1-13.

Shomura, R. S., and W. M. Matsumoto. 1982. Structured flotsam as fish aggregating devices. NOAA-TM-NMFS-SWFC-22, 9 p.

Westerberg, H. 1982. Ultrasonic tracking of Atlantic salmon. I. Movements in coastal regions. Rep. Inst. Freshwater Res. Drottningholm 60: 81-101.

Yuen, H. S. H. 1970. Behavior of skipjack tuna, *Katsuwanus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Board Can. 27(11):2071-2079.

Yuen, H. S. H., A. E. Dizon, and J. H. Uchiyama. 1974. Notes on the tracking of the Pacific Blue Marlin, *Makaira nigricans*, p. 265-268. *In* R. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12-72, Part 2. NOAA Tech. Rep. NMFS-SSRF 675.

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PROGRESS REPORT ON TUNA TRACKING

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National Marine fisheries Service
Honolulu, Hawaii

This is a brief, informal summary of the results from the first year of our tracking research. We have achieved the two goals we set for the first year, namely to: (1) outfit the vessel with all the equipment and modifications necessary for the programme, and (2) begin collecting data. We are very pleased with the data so far obtained and we anticipate a substantial increase in the number of tracks acquired over the remaining year of the project. Our technique involves placing a depth sensitive ultrasonic transmitter on the back of the fish and then tracking it using a directional hydrophone mounted on our fisheries reseach boat.

So far, we have tracked eight fish: six are from around fish aggregation devices (FADs) and two tracks (one of six days duration) are from non-FAD fish that were caught on the 50 fathom curve inshore from the FAD locations. These non-FAD tracks will be used for comparison with FAD-associated fish. Two tracks are from bigeye tuna (_Thunnus obesus_), an increasingly important species for the fresh market, and six tracks are of yellowfin tuna (_T. albacares_). A full report will be available at the end of the project, but some aspects emerging from our data to date are:

1. The effective range of movement of yellowfin and bigeye tuna of 55-75 cm length around FADs appears to be approximately 6 to 10 miles. We tracked one fish that returned to a FAD after making a 13-mile loop (farthest distance from FAD 6.5 miles) over 24 hours (figure 1). On another occasion, a yellowfin tuna tagged at "S" FAD proceeded directly to "V" FAD about 10 miles away. This track shows that (a) the range of influence of a FAD is at least 10 miles, (b) fish can learn the location of two FADs, and (c) these animals have the navigational capabilities to move from one small area to another (figure 2).

2. Yellowfin tuna have "home ranges" that they retain over at least several days. A fish caught on the 50 fathom contour returned to his area every day following nighttime excursions offshore (figure 3). This track also demonstrates that not all tuna in an area associate regularly with FADs because this animal passed by "V" buoy several times without actually visiting it.

3. One track of a yellowfin tuna arriving at a FAD indicates that 85% of the time spent at the FAD was on the up-current side (figure 4). This behaviour raises some fascinating questions with regard to the underlying mechanisms of fish orientation. This type of information may also prove very useful to fishermen regarding the techniques they use to fish around floating objects. We obviously need to replicate these tracks to be more certain of our conclusions.

4. The vertical movement data are particularly interesting. Among other things, it appears that both yellowfin and bigeye have "travelling depths" that they use when moving from one place to another. Daytime travelling depths for yellowfin appear to be at the bottom of the mixed layer (figure 5) whereas bigeye run much deeper. It is interesting to note the very consistent travelling depths (and temperatures) of the bigeye and also the extremely regular upward excursions (figures 6 and 7). These constant "travelling depths" may be of great value to longline and handline fishermen if additional data can be acquired. Both species swim much closer to the surface at night.

We intend to continue to track fish associated with FADs and a more thorough analysis of their movements will be forthcoming. We hope to acquire funding to expand the project in the future to include larger fish and additional species such as skipjack tuna (Katsuwonus pelamis) and mahimahi (Coryphaena hippurus). In this way, we will determine if the larger (more valuable) yellowfin and bigeye tuna have the same habits as the small/medium fish that we are now tracking and we will also be able to construct a detailed picture of how the several important pelagic species interact, divide the oceanic food resource, and orient around floating objects such as FADs and logs.

This research is being supported by Hawaii Institute of Marine Biology, University of Hawaii; Sea Grant College, University of Hawaii; National Marine Fisheries Service (Honolulu); and the Federation of Japan Tuna Fisheries Co-operative Association.

Footnote: since this report was prepared, a fisherman caught one of our fish carrying a transmitter three weeks after we abandoned it. The fisherman caught the fish trolling, and said that it was healthy and put up a good fight. This anecdote supports our claim that the transmitter does not seriously impair the animal's behaviour.

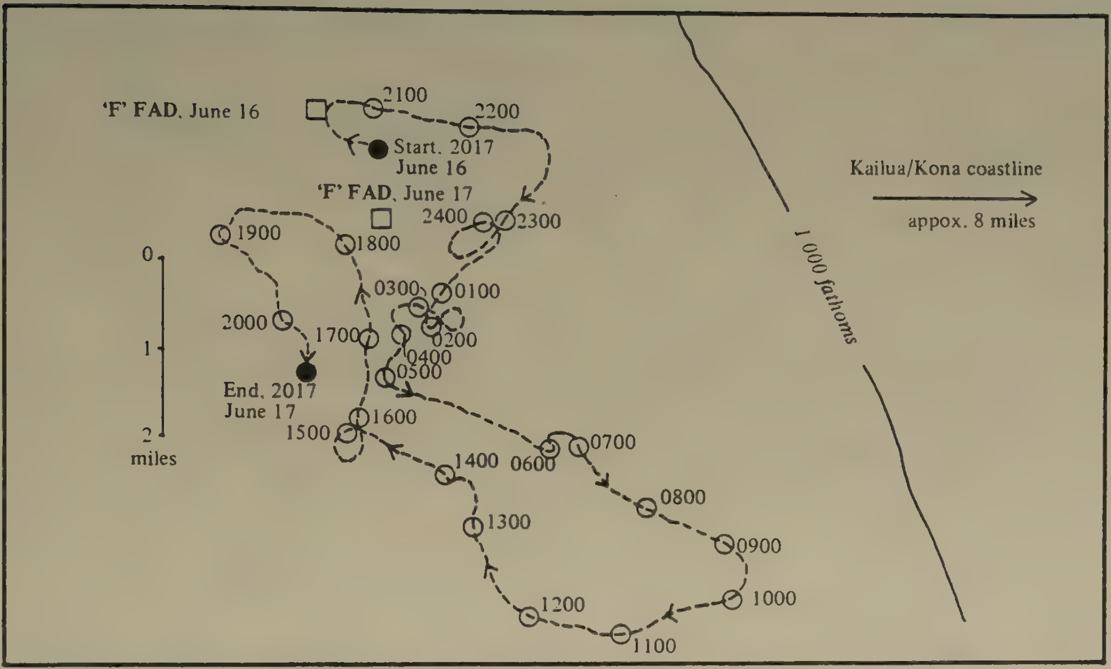
'F' FAD, June 16
2100
2200
Start, 2017
June 16
'F' FAD, June 17
2400
2300
1900
1800
0
1
2
miles
0300
0100
2000
1700
0200
0400
0500
End, 2017
June 17
1600
1500
1400
0600
0700
0800
1300
0900
1000
1200
1100
1 000 fathoms
Kailua/Kona coastline
appox. 8 miles

Figure 1: Track of a bigeye tuna returning to FAD 'F' after a 13-mile loop. This animal (57 cm) was caught just after sunset near 'F' buoy and returned to the FAD at dusk the next day. Furthest distance from the buoy was about 6 miles.

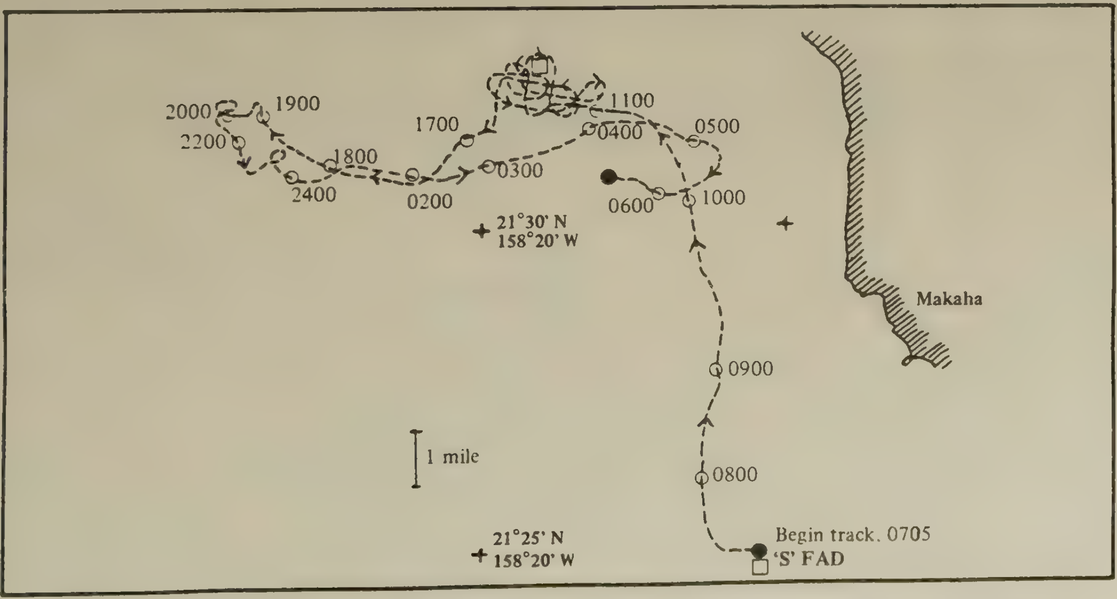
2000
1900
2200
1800
2400
0200
1700
0300
1100
0400
0500
0600
1000
21°30' N
158°20' W
Makaha
0900
1 mile
0800
21°25' N
158°20' W
Begin track, 0705
'S' FAD

Figure 2: A 55 cm yellowfin tuna caught at 'S' buoy was released after having an ultrasound transmitter placed on its back. The released fish moved in a very direct course to the next nearest FAD 'V' which was located about 9 miles away. After spending several hours near 'V' buoy, the fish moved offshore at night before returning the next morning.

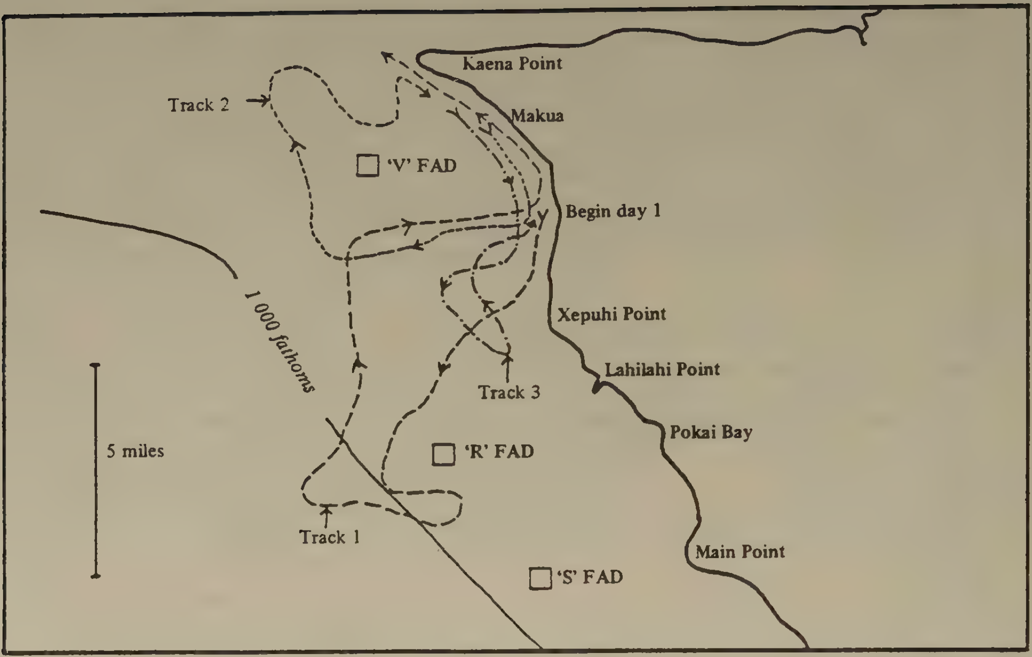
Track 2
Kaena Point
Makua
'V' FAD
Begin day 1
Xepuhi Point
Lahilahi Point
1 000 fathoms
5 miles
Track 3
Pokai Bay
'R' FAD
Track 1
Main Point
'S' FAD

Figure 3: Repetitive movements of a 70 cm yellowfin tuna during a six-day period. Three tracks of approximately 24 hours were made spanning a period of six days. During daylight hours, the fish patrolled the 50 fathom ledge between Kena Point and Makaha and made extensive excursions offshore after sunset. The path of its night-time movements took it beyond the location of the adjacent FADs. FAD 'R' was not on station at the time of these tracks.

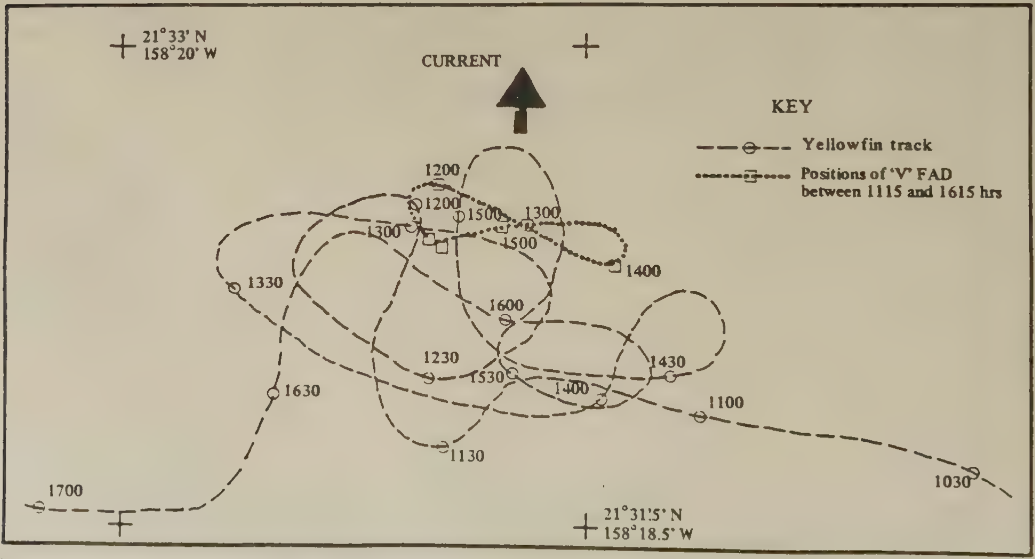
21°33' N
158°20' W
CURRENT
KEY
Yellowfin track
Positions of 'V' FAD between 1115 and 1615 hrs
1200
1200
1500
1300
1300
1500
1400
1330
1600
1230
1530
1430
1400
1100
1630
1130
1700
1030
21°31.5' N
158°18.5' W

Figure 4: After arriving at FAD 'V', a 55 cm yellowfin tuna spent about 85 per cent of the next 5 hours on the up-current side of the buoy. The movements of the buoy were also recorded using Loran-C and radar data.

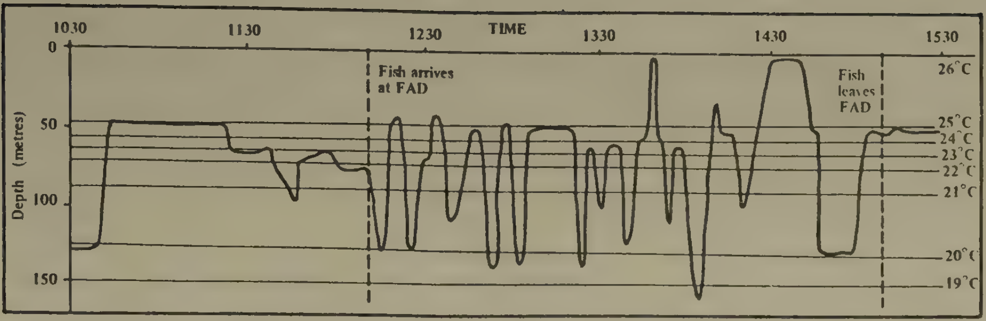

Figure 5: Vertical movements of a yellowfin tuna approaching and staying at a FAD. When moving from one location to another, yellowfin tuna appear to utilise 'travelling depths' at which they spend extended periods of time. A frequently observed travelling depth appears to be the boundary between the bottom of the mixed layer and the top of the thermocline (in this case 25°C at about 50 metres). This fish exhibits a travelling depth while approaching the buoy and then displays quite regular vertical movements when in the immediate vicinity of the FAD. Again, these vertical excursions are frequently limited by the mixed layer boundary and the 20°C isotherm.

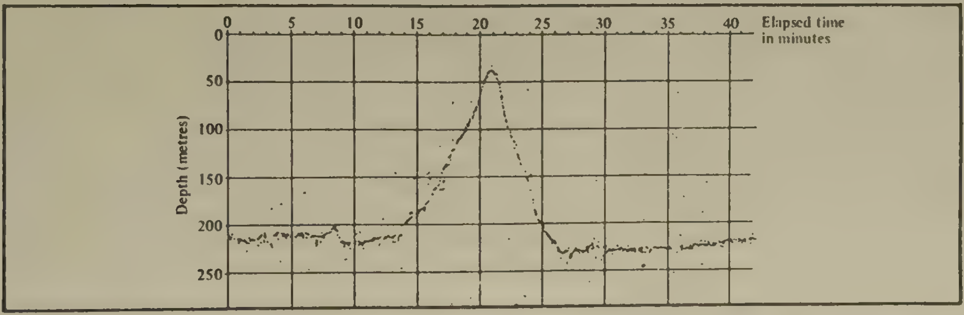

Figure 6: The swimming depth of this 54 cm bigeye tuna was constant around 200 metres during the daytime. However, the fish also displayed dramatic upward excursions which occurred at very regular hourly intervals during daytime. This figure also displays the fine detail our system allows.

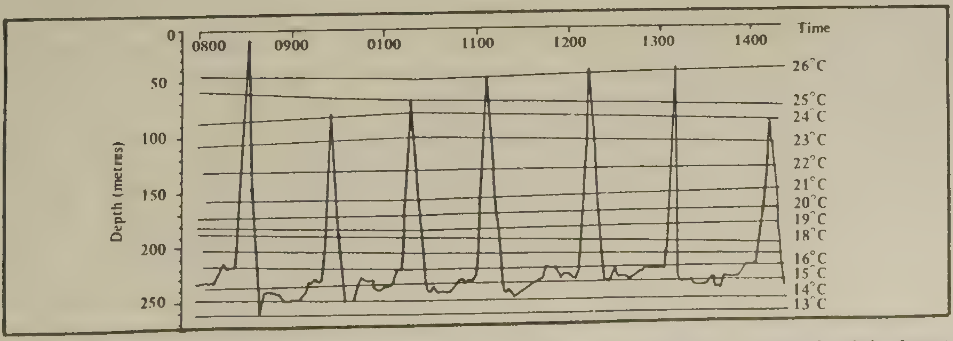

Figure 7: Predominant daytime travelling depth of a 57 cm bigeye tuna. The travelling depth is almost completely restricted to the 14-16°C stratum at 230-250 metres. This plot also shows the very regular upward excursions that seem to be characteristic of this species and size.

Recreational Albacore, *Thunnus alalunga*, Fishery by U.S. West Coast Commercial Passenger Fishing Vessels

DAVE HOLTS

Introduction

The commercial passenger fishing vessel (CPFV) industry along the west coast of the United States is a multimillion dollar business which contributes major economic and social benefits. The vessels include charter boats for hire by individuals or groups as well as partyboats with a first come, open seating policy. Commercial passenger fishing vessel owners and operators from the Mexican border to Puget ound gross millions of dollars annual- y providing the fishing enthusiast an opportunity to "get away" and enjoy a ecreational fishing experience that would not otherwise be available. Well ver 1 million angler trips are logged by hese west coast anglers each year. The PFV albacore, *Thunnus alalunga*, port catch represents from 1 to 3 per- ent of the North Pacific commercial bacore catch and a significant portion f the southern California recreational atch.

Background

The albacore is a valuable commer- al species with annual North Pacific ndings (Table 1) in excess of 75,000 etric tons (t). To the sportsman, alba- re is a highly prized, migratory game- sh which contributes significantly to e southern California sport fishing in- stry during the summer and fall onths. In northern California, Wash- gton, and Oregon, where the coastal arter boat fishery focuses on Pacific lmon, *Oncorhynchus* spp., the alba- re fishery is much less significant and the catch fluctuates considerably from year to year (Table 2).

Albacore Movements

Annual transpacific albacore migrations have been described in detail by Clemens (1961), Otsu and Uchida (1963), Clemens and Craig (1965), and Laurs and Lynn (1977). Albacore moving eastward across the North Pacific are exposed to commercial fisheries of several nations which use a variety of fishing gears. Domestic catch records indicate that commercial quantities of albacore first appear off the coast of Baja California, Mexico, and southern California in mid-June and early July. The albacore continue to move into coastal waters and northward in response to the warming of the surface waters and normally reach the offshore waters of Oregon and Washington by the end of July.

Several temperature-related factors play an important role in determining the major times and areas of albacore abundance and availability to a surface fishery along the Pacific coast. Periods of anomalous warm water, such as the El Niño events of 1959, 1972, and 1983, affect the distribution of albacore (Squire, 1983) as do seasonal variations in magnitude of coastal upwelling in the Pacific Northwest (Lane, 1965). The southern California albacore sport catch is greatest when surface waters are from 18.3° to 19.7°C (Squire, 1982); commercial fishing activity peaks along the entire coast from 17.2° to 18.9°C (Majors et al.[1]).

Rapid changes in the thermal structure are also important to the distribution and availability of albacore. Albacore tend to aggregate in the vicinity of ocean fronts. When these fronts are well developed, they may influence migration patterns and increase albacore catch rates in those areas (Laurs and Lynn, 1977). The strength and depth of the thermocline are also important to the availability of albacore. Recent tagging studies using acoustic transmitters indicate albacore swim near the bottom of the mixed layer during the day, but at sunset they begin making frequent vertical excursions near the surface which continue throughout the night (Laurs et al.[2]). Water turbidity and the amount of freshwater discharge flowing south from the Columbia River influence albacore availability off Oregon (Owen, 1968).

The Fleet

The CPFV fleets are located near major coastal metropolitan areas from which their clientele can be drawn. For albacore, they must also be located within a few hours running time of consistently good fishing grounds (Fig. 1). Consequently, the size, speed, and comfort of these vessels are important in attracting customers. Southern California passenger vessels are larger than those in northern California, Oregon, and Washington. These sport boats currently targeting on albacore are from 60 to 117 feet long and average 70 feet in length. There has also been a continuing trend in recent years to larger and more com-

ve Holts is with the Southwest Fisheries Center, tional Marine Fisheries Service, NOAA, P.O. x 271, La Jolla, CA 92038.

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[1] Majors, A. P., A. L. Coan, N. Bartoo, and F. Miller. 1982. Summary of 1981 North Pacific albacore fishery data. NMFS Southwest Fish. Cent., La Jolla, Calif. Admin. Rep. LJ-82-12, 35 p.

[2] Laurs, R. M., R. J. Lynn, R. C. Dotson, R. Nishimoto, K. Bliss, and D. B Holts. 1982. Exploratory albacore longline fishing in the eastern North Pacific during winter 1982. NMFS Southwest Fish. Cent., La Jolla, Calif. Admin. Rep. LJ-82-06, 79 p.

Table 1.—Catches of North Pacific albacore in metric tons, 1952-1983.

Year	Japan					Taiwan	United States				Canada	Grand total[6]
	Pole-and-line[1]	Longline[2]	Gillnet	Other gear	Total	Longline	Baitboat	Jibgoat[3,4]	Sport[5]	Total	Jigboat	
1952	41,386	26,687		237	68,710			23,843	1,373	25,216	71	93,997
1953	32,921	27,777		132	60,830			15,740	171	15,911	5	76,746
1954	28,069	20,958		38	49,065			12,246	147	12,393		61,458
1955	24,236	16,277		136	40,649			13,264	577	13,841		54,490
1956	42,810	14,341		57	57,208			18,751	482	19,233	17	76,458
1957	49,500	21,053		151	70,704			21,165	304	21,469	8	92,181
1958	22,175	18,452		124	40,731			14,855	48	14,903	74	55,708
1959	14,252	15,502		67	30,121			20,990	0	20,990	212	51,323
1960	23,156	17,369		76	42,601			20,100	557	20,657	5	63,263
1961	18,636	17,437		268	36,341		2,837	12,054	1,355	16,246	4	52,591
1962	8,729	15,764		191	24,684		1,085	19,753	1,681	22,519	1	47,204
1963	26,420	13,464		218	40,102		2,432	25,142	1,161	28,735	5	68,812
1964	23,858	15,458		319	39,635	26	3,411	18,389	824	22,624	3	62,283
1965	41,491	13,701		121	55,313	16	417	16,461	731	17,609	15	72,953
1966	22,830	25,050		585	48,465	16	1,600	15,169	588	17,357	44	65,882
1967	30,481	28,869		520	59,870	17	4,113	17,814	707	22,634	161	82,682
1968	16,597	23,961		1,109	41,667	15	4,906	20,441	951	26,298	1,028	69,008
1969	32,107	18,006		1,480	51,593	21	2,996	18,826	358	22,180	1,365	75,157
1970	24,376	15,372		956	40,704	23	4,416	21,039	822	26,277	354	67,358
1971	53,198	11,035		1,262	65,495	24	2,071	22,496	1,175	25,442	1,587	92,548
1972	60,762	12,649	1	921	74,333	25	3,750	23,600	637	27,987	3,558	105,903
1973	69,811	16,059	39	1,883	87,792	35	2,236	15,652	84	17,972	1,270	107,059
1974	73,576	13,053	224	1,065	87,918	40	4,777	20,177	94	25,048	1,207	114,213
1975	52,157	10,060	166	402	62,785	28	3,243	18,926	640	22,809	101	85,723
1976	85,336	15,896	1,070	1,394	103,696	37	2,700	16,314	713	19,724	252	123,712
1977	31,934	15,737	688	1,039	49,398	561	1,497	10,012	537	12,046	53	62,058
1978	59,877	13,061	4,029	3,209	80,176	53	950	15,700	810	17,451	23	97,712
1979	44,662	14,249	2,856	1,280	63,047	81	303	6,253	74	6,630	289	70,049
1980	46,743	14,660	2,986	1,516	65,905		382	7,599	168	8,149	212	74,349
1981[7]	27,426		17,425				784	12,280	195	13,259	200	
1982[7]							425	6,661	257	7,086	1	
1983[7]							607	9,512	87	10,119	115	

[1] Japanese pole-and-line catches include catches by research vessels.

[2] Japanese longline catches for 1952-60 exclude minor amounts taken by vessels under 20 gross tons. Longline catch weights are estimated by multiplying annual number of fish caught by average weight statistics.

[3] U.S. jigboat catches include minor amounts taken by baitboats not submitting logbooks.

[4] Jigboat catches for 1952-60 include baitboat catches.

[5] U.S. sport catch is a minimum estimate based on partial coverage.

[6] Grant totals omit unknown but minor catches by longline and pole-and-line vessels of the Republic of Korea.

[7] Figures for 1981-83 are preliminary.

Table 2.—Recreational albacore partyboat catch for all available data in number of fish and metric tons.

Year	California[1]		Oregon	Washington[2]		Total	
	No. fish	t		No. fish	t	No. fish	t
1947	11,445	84				11,445	84
1948	15,414	113				15,414	113
1949	22,692	166				22,692	166
1950	118,087	866				118,087	866
1951	75,924	557				75,924	557
1952	187,267	1,373				187,267	1,373
1953	23,363	171				23,363	171
1954	20,098	147				20,098	147
1955	78,688	577				78,688	577
1956	65,814	482				65,814	482
1957	41,540	304				41,540	304
1958	6,482	48				6,482	48
1959	39	—[3]				39	—[3]
1960	76,075	557				75,075	557
1961	184,981	1,355				184,981	1,355
1962	229,314	1,681				229,314	1,681
1963	158,372	1,161				158,372	1,161
1964	112,358	824				112,358	824
1965	99,771	731				99,771	731
1966	74,680	588				74,680	588
1967	96,497	707				96,497	707
1968	129,710	951				129,710	951
1969	48,887	358				48,887	358
1970	112,106	822				112,106	822
1971	160,361	1,175				160,361	1,175
1972	86,890	637	—[4]		—[4]	86,890	637
1973	9,858	72	—[4]	1,648	12	11,506	84
1974	12,814	94	—[4]		—[4]	12,814	94
1975	81,562	595	—[4]	5,494	45	87,056	640
1976	84,973	620	—[4]	9,566	93	94,529	713
1977	70,274	513	—[4]	4,275	24	74,549	537
1978	92,646	676	—[4]	20,137	134	112,783	810
1979	10,196	74	—[3]		—[3]	10,196	74
1980	21,309	156	—[3]	1,540	12	22,849	168
1981	26,648	195	—[3]		—[4]	26,648	195
1982	36,690	268	—[3]		—[3]	36,743	268
1983	17,161	125	—[3]		—[3]	17,161	125

[1] DFG landings converted to metric tons using 16.1 pounds average fish weight.

[2] Estimated from landing weights of locally caught commercial fish.

[3] Minimal catch reported less than 5 t

[4] Sport catch reported but no sampling effort.

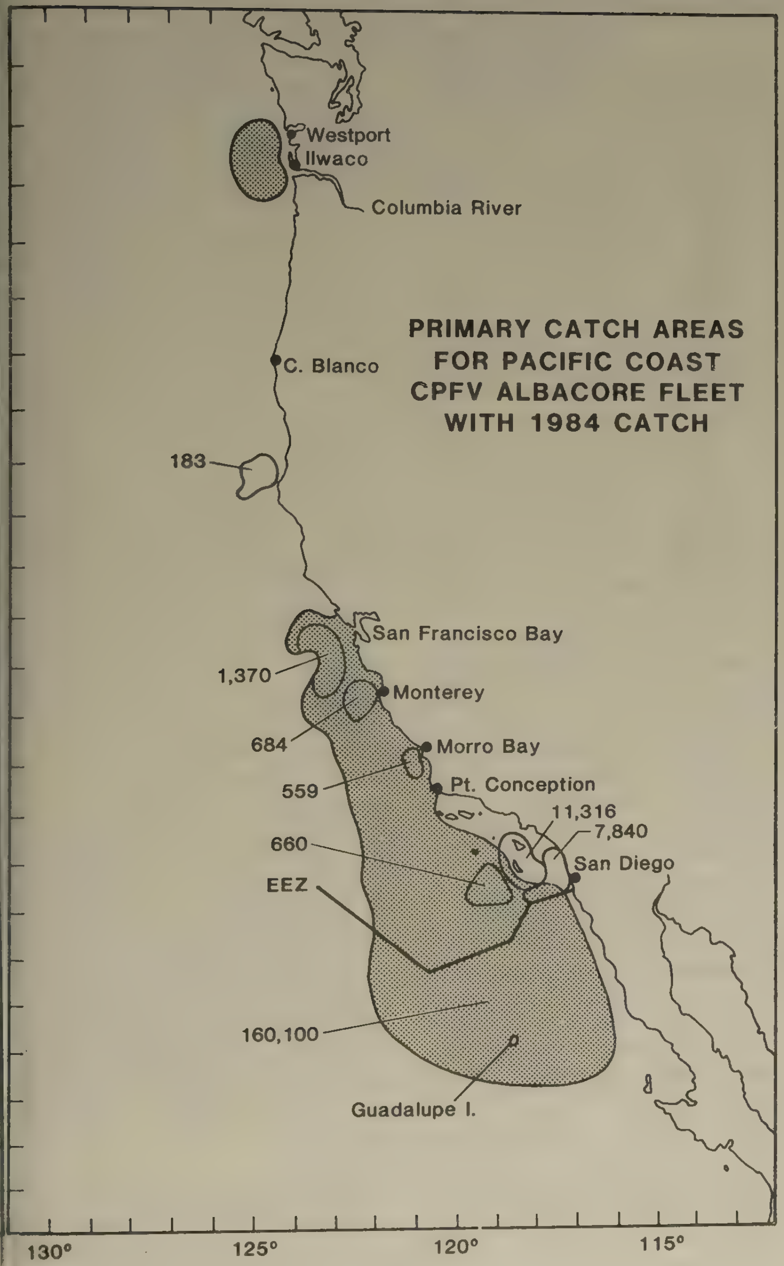

Figure 1.—Primary catch areas for the CPFV albacore fleet.

table vessels. In 1978, only 26 per-
nt of the southern California vessels
eeded 65 feet and a few exceeded 100
t, while only 5 percent of the central
d northern California vessels exceed
feet (Gruen, Gruen, and Associ-
s³).

Charter boats fishing for albacore off Oregon and Washington are temporarily drawn from the recreational Pacific salmon fishery and operate for albacore only when large quantities are close to shore. During the middle 1970's these vessels averaged 46 feet and none exceeded 65 feet in length (Lincoln and Culver, 1977). There has been continual upgrading of vessels in this fleet over the past several years; however, no large vessels have been able to move permanently into the fleet, and the size composition has not changed appreciably.

The most common fishing methods employed by the CPFV's include live bait fishing and trolling with lures and feather jigs (Dotson, 1980; Culver, 1977). Some regional variation in specific techniques has been developed to optimize local catches. For example, anglers in southern California normally troll with lures and feather jigs to locate areas of fish and then throw live anchovies in the water as chum to attract and hold the albacore at the boat while fishing with baited hooks. Jig fishing is more common in Washington and Oregon where the sportboats are usually salmon charter boats; however, many of these boats carry live bait on albacore trips. These boats are typically 25-55 feet long and carry only 6-12 passengers on 1-day trips. Albacore trips are usually scheduled only when strong local fishing is reported by commercial fishermen.

Regional Catch Information

Catch information from the CPFV fleet is collected by the individual state under whose jurisdiction the vessels operate. Each state has a survey program designed to sample the CPFV catch and to identify the economic importance of the major fisheries. The quantity and quality of statistics collected by the individual state agencies are highly variable, depending on the popularity of target species, economic importance of the species, status of targeted stocks, and political importance to a particular region.

California

Albacore, along with bluefin tuna,

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[3] Gruen, Gruen, and Associates. 1979. The California commerical passenger fishing vessel and southern California live bait industries. NMFS Southwest Fish. Cent., La Jolla, Calif. Admin. Rep. LJ-79-31C, 83 p.

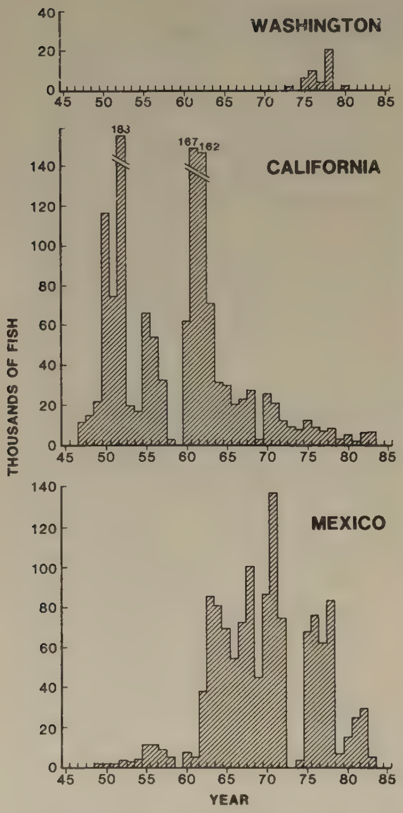

Figure 2.—Albacore catch from the waters off Mexico, California, and Washington.

Table 3.—Pacific Coast CPFV albacore catch (number of fish) and effort (C/A) by region.

			California								
	Mexico		San Diego to Pt. Conception		Pt. Conception to Oreg. border		Total		Oregon (No. of fish)	Washington	
Year	No.	C/A	No.	C/A	No.	C/A	No.	C/A		No.	C/A
1936-61	10,365	2.72	35,187	1.00	1,568	1.29	47,120	1.17			
1973	19		9,839				9,858			1,648	2.23
1974	3,850		8,964				12,814				
1975	68,296		13,266				81,562			5,494	3.40
1976	76,268		8,705				84,973			9,566	3.09
1977	62,678	1.65	6,504	1.58	1,092	0.66	70,274	1.60		4,275	1.77
1978	84,080		8,566				92,646			20,137	3.67
1979	7,260	1.50	1,021	0.61	1,915	1.01	10,196	1.21			
1980	15,657	1.36	1,290	1.93	4,362	1.08	21,309	1.32		1,540	3.08
1981	24,702	1.17	1,272	0.56	674	2.05	26,648	1.16			
1982	28,862	1.26	5,071	1.12	1,214	2.04	35,147	1.26	35	18	
1983[1]	8,968	1.84	2,990	2.05	5,203	2.21	17,161	1.98	0	0	

[1] Preliminary

Thunnus thynnus, were first reported taken in a sport fishery off Santa Catalina Island, Calif., at the turn of the century (Young, 1969). San Diego sport boats began traveling into the more productive Mexican waters (Fig. 2) in the middle 1950's for albacore, yellowtail, *Seriola lalandi*; white seabass, *Atractoscion nobilis*; Pacific barracuda, *Sphyraena argentea*; and billfish (Istiophoridae and Xiphiidae). The size, speed, and luxury of the southern California sport boats grew in response to these newly found areas off Baja California with some albacore vessels traveling as far as Guadalupe Island, 220 miles south of San Diego. The Channel Islands, nearby outer banks, and local Mexican waters all provide seasonally good albacore fishing for 1- and 2-day trips. These areas are only 30-80 miles offshore and sea conditions are normally favorable during the summer and fall months. Weather and sea conditions are commonly unfavorable north of Point Conception, Calif., because of the shorter warm-water periods and stronger prevailing winds that produce rougher seas for fishing.

The California Department of Fish and Game (CDFG) has required CPFV operators to maintain accurate records of their catch and number of passengers since 1936. Baxter and Young (1953) reported on the accuracy of some of these early records and found that albacore (also lingcod, *Ophiodon elongatus*; Pacific salmon, and yellowtail) counts were accurate over the 5-year study period (1947-51). They concluded that the high degree of accuracy was a result of the desirability of albacore, and that they were caught in relatively small numbers. By 1968, anglers frequenting southern California sport boats rated albacore the most desirable sport fish, and CPFV operators rated albacore seventh in overall importance to their business (Young, 1969).

California's historic albacore sport catch (1936-61) indicates an annual average of 41,000 albacore caught by 40,246 anglers. The catch per angler-trip (C/A) over this period averaged 1.17 with a range from 0.3 to 3.3 C/A (Clemens and Craig, 1965). Albacore effort data for 1936-61 have been merged with the data of other species taken in the same area and time period. Original records for many of these effort data are currently not available.

California anglers annually averaged 151 t (20,667 fish) between 1979 and 1983. The known number of albacore caught and the number caught per angler-trip for California, Oregon, and Washington are shown in Table 3. In southern California, albacore sportfishing dominates much of the CPFV fleet during summer and early fall. California's albacore sportfishing effort from 1979 to 1983 was conducted in the local Mexican waters; 11.3 percent occurred off southern California, and 10.6 percent occurred north of Point Conception. In contrast, records from 1936 to 1961 reveal that about 90 percent of the California effort occurred in southern California waters and 10 percent in Mexican waters, with almost no effort to the north.

Washington

The albacore CPFV fishery in Washington, which began in the early 1970's, was an offshoot of the very successful salmon charter boat fishery. The number of trips for ocean-going salmon began increasing rapidly in the late 1940's, and by early 1960's sportfishing expenditures were the single most important element in the local economy of several of Washington's coastal marine communities (Crutchfield and MacFarlane, 1968). By 1975, coastal salmon harter boats exceeded 500,000 angler rips annually and had long since passed ne effort expended by private boats Phinney and Miller, 1977). This large, uccessful fishery provided the foundaion for Washington's albacore charter oat fishery which began off Grays Haror and the mouth of the Columbia iver in 1970. Vessel owners found that ne nearshore availability of albacore rovided local saltwater anglers with ood summer albacore fishing through 978. This resource also served to boost agging charter boat revenues brought n by decreasing salmon catches and inreasing regulations.

Washington's first recreational albaore catch statistics were reported in 973. In 1975, the Washington Departnent of Fisheries (WDF) began a surey to evaluate the importance of this ew fishery. Catch and effort data (Table) were collected at the two southern oastal ports of Westport and Ilwaco Lincoln and Culver, 1977). Survey data vere not collected in 1974, although a noderately active charter boat fishery id occur. During the period for which ata have been reported (1973-78), a total f 41,110 albacore weighing 308 t were anded in 13,344 angler trips, averaging .08 albacore per angler trip (C/A). No atch data were reported for 1979 and nly 500 angler trips were reported for 980. In both 1981 and 1982, albacore id not appear inshore. Consequently, nly a few exploratory trips were scheuled and these were unproductive. The igh angler catch rate observed when ish were present indicates a successful lbacore sport fishery will develop any time albacore migrate within range of Washington's charter boats.

Oregon

Like Washington, the growth of Oregon's charter boat industry has long depended on various species of Pacific salmon (Wendler, 1960). Over 81,000 angler trips are logged annually for salmon; only a few have ever been reported for albacore.

Local nearshore upwelling normally displaces albacore too far offshore for Oregon's charter boats. Predominant northern winds in summer and fall transport surface waters offshore, allowing nearshore upwelling of colder waters. Lane (1965) found that, while it is a complex system, a breakdown of the normal wind patterns can result in a cessation of coastal, coldwater upwelling. As a result, albacore can move into these nearshore regions where they become available to local charter boats. Owen (1968) found that in addition to the general wind direction, the discharge of fresh water from the Columbia River into coastal and offshore areas affects albacore distribution and availability. A relatively weak upwelling was reported in 1976 (PMFC, 1977) and the Oregon Department of Fish and Wildlife (ODFW) reported that a small, opportunistic charter boat fishery for albacore developed during 1975 and 1976 (ODFW, 1977).

Interest in this sport fishery continued in 1977 and 1978 as albacore again became available 20-60 miles off Coos Bay and north to the mouth of the Columbia River. Some charter boats reported catches of up to five albacore, weighing from 15 to 20 pounds, per angler trip (PMFC, 1978). Nearshore availability has been lower since 1978 with few charter boat trips scheduled. Recent ODFW statistics indicate that only about 50 albacore were taken in 1980 and 24 in 1981. In 1982, five charter boats reported a total catch of four albacore. Oregon's sportsmen have demonstrated their interest in albacore and will certainly participate in a CPFV fishery when the fish come within 50 miles of shore.

Discussion

The commercial albacore fleets of at least five countries catch more than 70,000 t of albacore annually from the North Pacific. The U.S. Pacific coast albacore sport fishery lands less than 1 percent of the total commercial catch. Economists, however, have shown in some detail the importance of recreational fishing to regional economic growth, as well as the recreational benefits to the sportsman (Wendler, 1960; Holliday et al., 1984; Center for Natural Areas[4]).

In 1982, San Diego albacore fishermen made nearly 28,000 angler trips and spent over $1.5 million dollars on sportboat (CPFV) fees alone. The commercial value of this catch was less than $200,000. Additional revenues realized by local merchants for tackle, bait, fuel, food, and lodging have not been determined for the recreational albacore fishery, but they are significant during the season. The historic value and importance of the recreational albacore catch in northern California, Oregon, and Washington are practically undocumented. Washington's record of fishing effort in the middle 1970's was well documented, but no information exists for the periods when fishing was less than spectacular.

The tremendous fluctuation in Pacific coast CPFV catch rates is due to environmental factors that influence the

Table 4.—Washington albacore sport catch and effort reported for 1973 and 1975-78[1].

Year	No. of albacore	Total weight[2] (t)	No. of angler trips	Albacore per angler trip	No. of angler hours	Albacore per angler hour	Port sampled
1973	1,648	12.0	739	2.73			Westport
1975	5,494	45.0	1,615	3.40	10,873.9	0.51	Ilwaco
1976	947	9.2	720	1.03	5,185.1	0.16	Ilwaco
1976	8,609	83.5	2,373	3.63	21,183.0	0.41	Westport
1977	976	5.5	977	1.00	5,483.9	0.18	Ilwaco
1977	3,299	18.7	1,432	2.30	1,096.2	0.31	Westport
1978	5,748	38.2	1,796	3.20			Ilwaco
1978	14,389	95.7	3,692	3.90			Westport
Total	41,110	307.8	13,344	3.08	43,822.1	0.44	

[1]Adapted from Lincoln and Culver, 1977.
[2]Weights calculated from local commercial landings.

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[4]Center for Natural Areas. 1980. Survey of partyboat passengers to summarize and analyze recreational demand for partyboat fishing in California. NMFS Southwest Fish. Cent., Admin. Rep. LJ-80-14C, 47 p.

nearshore distribution and surface availability of albacore. They normally begin moving into coastal Mexican and southern California waters in June as the waters warm to 15° - 18°C; and southern California vessels have little trouble reaching good fishing areas. North of Point Conception, Calif., albacore are present normally from mid-July through early September. Coastal upwelling of colder, deep ocean water and generally harsher oceanographic conditions combine to displace albacore beyond the range of the small, troll-type charter boats of northern California, Oregon, and Washington.

The anomalous warming periods in the eastern Pacific, known as El Niño, also disrupt the normal albacore distribution and migratory paths (Squire, 1983). This was particularly evident in 1959 when the fish did not move into southern California waters at all, and again in 1973 when the CPFV catch feel from a 5-year mean of more than 100,000 fish to less than 10,000 fish. It was during this latest period that Oregon and Washington charter boats did well on albacore around Grays Harbor and the mouth of the Columbia River. Oregon's charter boats worked these albacore schools, but effort was low compared with their other recreational fisheries and consequently was not included in their State Fisheries Census. The Washington Department of Fisheries found good activity and public interest in sustaining an albacore sport fishery, and several years of good catch and effort data were collected. Additionally, these El Niño years and those immediately following were excellent for the Oregon and Washington commercial jig boats, whose landings were well above average. The sport fishery failed in recent years due to a lack of fish within about 80 miles of shore.

The anomalous warming of 1976 was weak and short lived compared with those of 1972-73 and 1982-83 and consequently had little effect on California's recreational albacore catch. The 1982-83 El Niño was considered strong, and southern California anglers caught relatively few albacore in waters that were 1° - 3°C above normal. The warm waters attracted a record number of yellowfin, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, however, and most traditional albacore sportboats switched their effort to these tropical species by the end of July. In contrast to the 1972-73 El Niño, the recent warming did not appear to encourage the Oregon and Washington albacore charter boat fishery.

California's historic (1946-61) catch rate of 1.17 C/A and the current 3-year average of 1.32 C/A are much lower than Washington's average of 3.08 C/A. Comparing these catch rates can be misleading because effort data are not available over the same time periods, and differing modes of operation tend to enhance Washington's catch rate. These northern charter boat operators schedule albacore trips only when there are local areas of warm water or a strong commercial fishery close to shore. This selective manner of scheduling fishing trips tends to boost their success rate even though they have shorter or even nonexistent seasons. In California, albacore sport boats can usually catch enough fish to attract passengers even when they have to spend a significant amount of time scouting. Southern California's sport boats also carry more passengers per boat, some of whom may not actually fish.

More complete information describing catch statistics and the economic importance of west coast CPFV fisheries, focusing on the larger and migratory gamefish, would be useful. A specific CPFV monitoring program throughout the Pacific Northwest would help to emphasize the local importance of those recreational fisheries as well as to identify to what extent they are altered by fluctuating environmental conditions.

Acknowledgments

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Literature Cited

Baxter, J. L., and P. H. Young. 1953. An evaluation of the marine sportfishing record system in California. Calif. Fish Game 38(3):343-353.

Clemens, H. B. 1961. The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951-1958. Calif. Dep. Fish Game, Fish Bull. 115, 128 p.

________ and W. L. Craig. 1965. An analysis of California's albacore fishery. Calif. Dep. Fish Game, Fish Bull. 128, 301 p.

Crutchfield, J. A., and D. MacFarlane. 1968. Economic valuation of the 1965-1966 salt-water fisheries of Washington. Wash. Dep. Fish., Res. Bull. 8, 57 p.

Culver, B. 1977. Albacore angling in Pacific Ocean waters off Washington State. Information Booklet 5, Wash. Dep. Fish. 21 p.

Dotson, R. C. 1980. Fishing method and equipment of the U.S. west coast albacore fleet. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-8, 126 p.

Holliday, M. C., D. G. Deuel, W. M. Scogin. 1984. Marine recreational fishery statistics survey, Pacific Coast, 1979-1980. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Curr. Fish. Stat. 8321, 224 p.

Lane, R. K. 1965. Wind, nearshore ocean temperature, and the albacore catch off Oregon. Fish Comm. Oreg. Res. Briefs 11(1):25-28.

Laurs, R. M., and R. J. Lynn. 1977. Seasonal migration of the North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: Distribution, relative abundance, and association with Transition Zone waters. Fish. Bull., U.S. 75(4):795-822.

Lincoln, R., and B. Culver. 1977. Washington's sport albacore fishery during 1975-76. Wash. Dep. Fish. Tech. Rep. 32, 22 p.

ODFW. 1976. 1975-76 Biennial Report. Oreg. Dep. Fish. Wildl., Portland, 18 p.

Otsu, T. and R. N. Uchida. 1963. Model of the migration of albacore in the North Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 63: 33-44.

Owen, R. W., Jr. 1968. Oceanographic conditions in the northeast Pacific Ocean and their relation to the albacore fishery. Fish. Bull., U.S. 66(3):503-526.

PMFC. 1977. 29th Annual Report for the year 1976 Pac. Mar. Fish. Comm., Portland, Oreg., 60 p

________ . 1978. 30th Annual Report for the year 1977. Pac. Mar. Fish. Comm., Portland Oreg., 63 p.

Phinney, L. A., and M. C. Miller. 1977. Status of Washington's ocean sport salmon fishery in the mid-1970's. Wash. Dep. Fish., Tech. Rep 24, 32 p.

Squire, J. L., Jr. 1982. Catch temperature for some important marine species off California. U.S Dep. Commer., NOAA-TM-NMFS-SSRF-759 19 p.

________ . 1983. Warm water and southern California recreational fishing: A brief review and prospects for 1983. Mar. Fish. Rev. 45(4-6) 27-34.

Wendler, H. O. 1960. The importance of the ocean sportfishery to the ocean catch of salmon in the states of Washington, Oregon, and California Calif. Fish Game 46:291-300.

Young, P. H. 1969. The California partyboat fishery 1947-1967. Calif. Dep. Fish Game, Fis Bull. 145, 91 p.

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Preservation of Northern Anchovy in Formaldehyde Solution

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ABSTRACT

Preservation and curation techniques used for northern anchovy, *Engraulis mordax*, taken in routine biomass surveys are described, and the effects of formaldehyde solution on length and weight are documented. Preservation in 10% buffered formaldehyde solution caused a 4% increase in anchovy wet weight after 24 h, but only negligible changes occurred over the next 340 d. Preservation also caused a 2% shrinkage in standard length after 24 h which increased to 3% after 340 d.

INTRODUCTION

The fish reproductive parameters used in the egg production biomass estimate (spawning fraction, female weight, batch fecundity, and sex ratio) are based on analysis of formalin-preserved specimens taken in trawl or purse seine collections. Careful attention to preservation and curation techniques is essential for an accurate measurement of these variables.

PRESERVATION

Histological analysis requires special care in preservation. Postovulatory follicles are relatively subtle histological structures, and poor preservation makes it impossible to stage them. Fish should be preserved while alive. Neither frozen specimens nor fish dead for some time can be used. A limited amount of biological material is preserved per collection container. We preserve only five adult anchovies per quart jar, roughly 80-150 g of tissue in 800 ml of formalin (see following). In all specimens, the body cavity is slit open along the side using a long incision to insure adequate preservation of the ovary. Care must be taken not to cut the ovary; this is difficult in females with hydrated eggs. If eggs are lost, they should be added to the jar.

To insure adequate preservation of the ovaries, we use a 10% buffered formaldehyde solution (formalin). Quantities of chemicals required for an 18-L container of buffered 10% formaldehyde preservative are as follows:

16.2 L distilled water
117 g sodium phosphate dibasic (granular, $Na_2H_2PO_4$)
72 g sodium phosphate monobasic (granular, $NaH_2PO_4 \cdot H_2O$)
1.8 L formaldehyde solution (37%).

Dissolve the sodium phosphate diabasic and stir in the distilled water; then mix in the sodium phosphate monobasic until dissolved, and finally add the formaldehyde solution.

Although Bouin's solution (Galigher and Kozloff 1971) might improve the quality of histological sections of ovarian tissue, its use is impractical for production work. Bouin's is more difficult to use on shipboard because represervation is required and because Bouin's preservation makes fecundity estimation difficult. Specimens preserved as described above are kept in the original preservative until curated, which may occur after as much as 2-3 mo of storage.

CURATION

A total of 15-25 females with active ovaries are removed from each collection in random order, blotted, weighed (nearest 0.1 g), and length measured (nearest 1 mm). We curate five more females per collection than needed for the spawning frequency estimate (see Picquelle 1985) in order to allow for females that will be rejected after histological analysis because of immaturity. (It is easier to curate a few additional females than to return to the original collection to process additional fish.) After a female has been weighed, the ovary is removed, blotted dry, and weighed to the nearest mg. Females may be discarded at this point, but the ovary is represerved in fresh buffered formaldehyde solution and stored individually in a vial. Ovaries that appear to be hydrated are noted, as are the presence and quantity of loose eggs in the jar. Each female is assigned a unique identification number (collection number plus fish number).

In female anchovy of 12 g or less, we consider ovaries immature when the ratio of ovary weight/female weight (less ovary) is 0.01. For females of 12 g or less, the probability of maturity is less than 5% when the gonad body weight ratio ⩽0.01 (Hunter and Macewicz 1980). These ovaries are stored in vials, but not processed histologically, regardless of the size of the ovary. Histological criteria are used to distinguish between immature and inactive ovaries in females heavier than 12 g (Hunter and Macewicz 1985).

Males are processed along with the females if a separate sample is not taken for sex ratio estimation (Picquelle 1985). If males and females are preserved together, fish must be taken randomly from the jars to maintain a random order by sex. Males are weighed until the combined total of male plus female weight in a single sample equals 500 g (the combined weight needed for sex ratio calculations), and thereafter no additional males are processed in that sample.

Table 1.—Effect of formalin preservation on standard length and wet weight of Northern anchovy preserved alive.

Elapsed time in formalin (Days)	Percent change from live measurement			
	Length (mean, 2×SE*)		Weight (mean, 2×SE*)	
1	−2.26	0.21	4.20	0.54
5	−2.44	0.24	4.20	0.59
10	−2.55	0.24	4.26	0.60
21	−2.81	0.24	5.40	0.74
42	−2.46	0.23	4.35	0.68
84	−2.27	0.21	3.70	0.74
341	−2.93	0.23	3.74	0.72

*Two times the standard error of the mean, where *n* for each sample = 55, except at elapsed time 21 days where *n* = 38.

EFFECTS OF PRESERVATION

The reproductive parameters used for biomass estimation are expressed in terms of live wet weight, but as the specimens are preserved in formaldehyde solution, a correction coefficient must be used.

The wet weight and length of 75 northern anchovy (ranging in weight from 2.6 to 27.0 g; mean weight 14.03 g) were determined when alive, 24 h after formaldehyde preservation, and at intervals over 340 d. Fifty-five fish were treated using the standard method described above (preserved alive with body cavity slit), 10 fish were first pithed, body cavity slit, and preserved while still alive, and 10 were pithed, slit, and allowed to die over a 20-min period before preservation.

In nearly all fish, the wet weight increased as a result of preservation. In only one of the 75 fish preserved was the wet weight after 85 d less than the initial live wet weight, and in only four fish was the weight the same. The increase in wet weight was minor. The mean increase in wet weight of the 55 fish preserved using the standard method was about 4%. In these fish, the total gain in wet weight occurred within 24 h after preservation and thereafter it remained about the same (Fig. 1). Pithed anchovy did not struggle in the preservative, and the initial weight gain after preservation was only 1%; but they gained weight steadily, attaining a 3% gain in 20 d and thereafter weight remained about the same. No difference existed between the two groups of pithed fish, indicating that death itself had no effect on subsequent weight in formalin. Struggling of live fish in formaldehyde solution appears to increase the initial rate of fluid uptake, but after 20 or more days the difference between fish preserved alive and those pithed or dead was 1% or less. This could cause a slight error in estimated live weight if some fish were preserved dead and others alive and the collection was curated immediately. For biomass estimation, we use the mean for all data on fish preserved alive (+4.3%). Most fish in our surveys are preserved alive and weighed 30-40 d later.

The length of all fish declined as a result of formalin preservation. Shrinkage after 24 h in preservative was 2% and increased to 3% after 340 d in preservative (Table 1). Shrinkage rates did not vary among the three treatment groups.

Similar effects of formalin preservation (shrinkage in length and gain in wet weight) were documented for salmon by Parker (1963), but plaice lost 9% of their wet weight when preserved in 4% formalin and sea water (Lockwood and Daly 1975), and Rosenthal and Westernhagen (1976) report no significant change in three species of siganids after formalin fixation. These and other studies (see reviews by Parker 1963, and Lockwood and Daly 1975) indicate that considerable variation exists with formalin preservation. Factors that account for this variation include species differences, fish size (life stage), state of the fish when preserved, duration of the fish in formalin, and ratio of formalin and dilutant. Among dilutants, fresh water is clearly preferable to sea water (Lockwood and Daly 1975). Clearly, the effects of formalin preservation are quite specific and calibration is required for any changes in technique, species, or life stage.

LITERATURE CITED

GALIGHER, A. E., and E. N. KOZLOFF.
1971. Essentials of practical microtechnique. 2d ed. Lea & Febiger, Philadelphia, 531 p.

HUNTER, J. R., and B. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 79-94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

LOCKWOOD, S. J., and C. de B. DALY.
1975. Further observations of the effects of preservation in 4% neutral formalin on the length and weight of 0-group flatfish. J. Cons. Int. Explor. Mer 36:170-175.

PARKER, R.
1963. Effects of formalin on length and weight of fishes. J. Fish. Res. Board Can. 20:1441-1455.

PICQUELLE, S.
1985. Sampling requirements for the adult fish survey. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 55-57. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

ROSENTHAL, H., and H. WESTERNHAGEN.
1976. Effect of formalin fixation on length, weight and condition factors of three siganid species. Arch. Fischereiwiss. 27(1):37-43.

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Measurement of Spawning Frequency in Multiple Spawning Fishes

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ABSTRACT

Methods for estimating the frequency of spawning in natural fish populations using histological criteria are described using the northern anchovy, *Engraulis mordax*, as an example. Illustrations and descriptions are provided of oocytes in mature ovaries, postovulatory follicles, and atretic follicles. Postovulatory follicles are used to estimate frequency of spawning, and atretic follicles (which may be confused with postovulatory follicles) are useful in estimating size at first maturity. Postovulatory follicles of four common commercial fishes, *Sardinops sagax*, *Merluccius gayi*, *Scomber japonicus*, and *Euthynnus lineatus*, are also described and illustrated. Methods for estimating spawning frequency other than ovarian histology are also discussed, as is testing of the assumption of determinate annual fecundity in multiple spawning fishes.

INTRODUCTION

The egg production method of biomass estimation requires an estimate of spawning frequency. This requirement exists because the method was developed for fishes, such as the northern anchovy, which have indeterminate annual fecundity. In such, the standing stock of advanced oocytes gives no indication of annual fecundity because new spawning batches are recruited from small, unyolked oocytes during the spawning season. Thus, the rate of egg production can be calculated only from estimates of spawning frequency and batch fecundity made during a survey period. On the other hand, in some multiple spawning boreal fishes, including haddock, *Melanogrammus aeglefinus*, and whiting, *Merlangius merlangus* (Hislop 1975; Hislop et al. 1978; Hislop[1]), and other fishes (Yamamoto 1956), the stock of oocytes destined to be spawned in a season is identifiable at the beginning of the season. In such fishes, annual fecundity may be considered to be determinate even though the fishes may spawn repeatedly during the season and the standing stock of advanced oocytes at the beginning of the season is considered to be equivalent to the annual fecundity. Hence, estimates of spawning frequency are unnecessary in fishes with determinate annual fecundity as long as the biomass survey includes the entire spawning period and nearly all of the stock of advanced oocytes are actually spawned. In some cases, not all the standing stock of oocytes are spawned and, consequently, potential annual fecundity is not realized during the spawning season. Documentation of the existence of determinate annual fecundity, and of its total utilization during the spawning season, is essential if the standing stock of oocytes is used to estimate spawning biomass. This is rarely done satisfactorily, and in a number of cases we believe the presumption of a seasonally determined fecundity is probably false which may lead to serious errors in biomass estimation. Estimation of the frequency of spawning and batch fecundity is one way to test the assumption of determinate annual fecundity.

The objective of this paper is to describe the methods for estimating frequency of spawning in natural fish populations. We begin with a brief discussion of histological methods, followed by a general description of the oocytes in an active ovary of northern anchovy, *Engraulis mordax*. We then describe the estimation of spawning frequency using aged postovulatory follicles (employed in the current method for biomass estimation of northern anchovy) and briefly discuss other methods. In the second section of the paper we discuss ovarian atresia, because histologists must be able to distinguish postovulatory follicles from atretic follicles, and knowledge of atresia is also necessary to separate postspawning females from immature ones. In the final sections we discuss tests of the assumption of determinate fecundity and future applications of histological classification of ovaries.

Most of the descriptions and all of the data in this paper are for the northern anchovy. Nevertheless we have tried to bring out important differences that may exist among species and to mention methodologies other than the ones we use for northern anchovy.

HISTOLOGICAL METHODS

All the techniques discussed in this paper involve, at least to some extent, histological examination of fish ovaries. In this section we briefly discuss the histological techniques used and comment on the procedures and time required to use histological classification for fish population work.

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[1] John R. G. Hislop, DAFS Marine Lab., P.O. Box 101, Victoria Road, Aberdeen AB9 8DB, Scotland, pers. commun. 25 Oct. 1983.

Histological preparation of tissues

Almost all northern anchovy ovaries histologically examined for postovulatory follicles were fixed in 10% neutral buffered Formalin (NBF), embedded in Paraplast, and 6-μm serial sectioned slides were made and stained by Harris' hematoxylin followed by Eosin counter stain. This procedure gave good results, and specific steps can be found in Luna (1968), Preece (1965), or most any histotechnique handbook. It is also possible to use resin embedding, sectioning on a rotary microtome, and Lee's Methylene blue-basic fuchsin staining (JB-4 Embedding Kit, Data Sheet No. 123, Polysciences, Inc., 1982). This technique may be preferable for small ovaries or small pieces of ovaries, although it is more difficult to get many serial sections and may not be practical for larger ovaries.

In addition to the instructions given in standard histotechnique texts, we found the following procedures and precautions to be useful in preparation of Hematoxylin and Eosin (H&E) sections of northern anchovy ovaries.

Fixation—Bouin's fixative gave better results than 10% NBF, but it required transferring ovaries into 70% ethanol within 1-2 d or the ovaries become hard and brittle. Transferring is possible in the laboratory but at sea it is often impractical. It is important to fix ovaries quickly and thoroughly, otherwise lysis or poor differentiation may occur. We insured proper exposure to fixative by slitting the abdomen of fish before fixing. In larger fish it is best to remove the whole ovary from the fish and preserve it separately. It is even better to cut a 1-cm section from the midsection and preserve it in ample fixative. Initial freezing of whole fish or ovaries is not recommended; fixation after freezing results in poor-quality H&E sections in which postovulatory follicles cannot be consistently identified, thus producing substantial errors in the estimation of spawning frequency. In addition, the process of thawing may cause lysis of hydrated oocytes.

Infiltration—Hardening of ovaries may occur if time spent in xylene or toluene is not kept at a minimum or if temperature of paraffin is not kept below 60°C.

Sectioning—It is necessary to have 10-20 good serial sections per slide for histological analyses. Cold (4°C) blocks and knives usually improve sectioning. If shattering occurs, it is possible to soak blocks (prefaced-off) in ice water for a short time (1-15 min) to improve sectioning with little or no shattering.

Mounting—Wiping slides with a very fine coat of Mayer's Albumen Affixative and drying mounted slides are often necessary to keep sections attached to slides. By mounting as many sections as possible on a slide, it may be possible later to microscopically trace questionable structures.

Staining—The standard procedure for Harris' Hematoxylin and Eosin staining is quick and easy, and results in good staining of postovulatory follicles. Initially a trial run is necessary to find out the optimal amount of time spent in each stain. Other stains, i.e., Mason's Trichrome, periodic acid-Schiff reagent, or Heidenhain's iron hematoxylin, can also be used except they often require more time or more elaborate techniques. These stains may be preferable for study of structures other than postovulatory follicles, for example, nuclear changes in oogenesis.

Rates of Processing and Classification

The production of slides depends largely upon the capacity of the automatic tissue infiltrator and the number of histotechnicians. In small research laboratories (infiltrator capacity = 30 samples per batch) production of 100-150 H&E slides (one ovary per slide) per week for one person is close to the maximum rate of production. Thus, for production work it is preferable to use commercial histological laboratories where H&E slides can be produced more quickly at a cost of (in 1983) about $4.00/slide.

The time required to classify each slide of ovarian tissue (about 10 sections per slide) depends upon the amount of detail recorded. If only spawning frequency is estimated (ageing postovulatory follicles and identification of hydrated oocytes), one person can classify about 1,000 slides in 25 d (8 h/d). Two to three times as much time is required if all other significant histological characteristics of the ovary are recorded, including the presence and abundance of alpha through delta stages of atretic yolked and unyolked oocytes and the relative abundance of oocyte classes. We have employed this detailed system over the years to provide a complete record of the condition of the ovary. However, our analysis indicates that the system can be simplified by identifying only hydrated oocytes, two age classes of postovulatory follicles, and by classifying ovaries into three atretic states (defined in a subsequent section). This reduces classification time per ovary to nearly the equivalent of that required to estimate only spawning frequency, yet the ability to identify major changes in atretic condition, and to separate postspawning females from immature females, is still maintained.

HISTOLOGICAL CHARACTERISTICS OF OOCYTES

The northern anchovy is a multiple spawning fish (Hunter and Goldberg 1980) with asynchronous oocyte development, i.e., oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). During the spawning season, oocyte development is a continuous process involving all stages of oocytes, with a new spawning batch maturing every week to 10 days in peak spawning months (Hunter and Leong 1981). The average female anchovy spawns at least 20 times per yr, yet within the ovary only 1-3 potential spawning batches of yolked oocytes exist and fewer than 10 potential batches exist when all oocytes >0.1 mm are included (Hunter and Leong 1981). Oocytes ≤0.1 mm constitute the reservoir of oocytes that are present in ovaries year-round in inactive as well as active ovaries. Little or no atresia occurs among oocytes in this size range. Thus, in anchovy spawning, batches must be recruited from the reservoir of oocytes ≤0.1 mm to account for the observed frequency of spawning. This means the fecundity of northern anchovy is clearly seasonally indeterminate.

Oocyte development and maturation in teleosts, reviewed recently by Wallace and Selman (1981), has been frequently subdivided into many stages (Yamamoto 1956; Lambert 1970b), but a simpler histological classification system seems appropriate for the purpose of this manual. We have combined the stages of past authors into four oocyte classes (unyolked, partially yolked, yolked, and hydrated), and we describe below for the northern anchovy the histological characteristics of each class.

Unyolked Oocytes

This class includes all oocytes without yolk that are between about 0.04 and 0.35 mm (Fig. 1a, b). Oocytes <0.04 mm are excluded because they consist mostly of "oogonial nests," have no true follicle layer, and appear not to undergo degeneration (Fig. 1b). The smaller oocytes within this class (0.04-0.15 mm) are spherical, have a large nucleus, and have cytoplasms that are narrow, homogeneous, and very densely stained with hematoxylin (Fig. 1b). A very thin, single layer of elongated, spindle-like cells (the beginning of the granulosa layer) surrounds these small oocytes. The large oocytes in this class are oval; their cytoplasm stains faintly with hematoxylin and has a cloudy, mottled appearance (Fig. 1d). The oval nucleus of these oocytes contains several nucleoli and is surrounded by a granular perinuclear zone. In these larger oocytes a thin, definite, hyaline membrane which has a faint eosinophilic stain (percursor of the zona radiata) appears between the oocyte and the growing follicle. The follicle consists of a narrow, single, inner layer of cuboidal granulosa cells and a single outer layer of flat elongated thecal cells with some blood capillaries. The larger oocytes also may have some small vesicles in the periphery of the cytoplasm. These vesicles are at times difficult to distinguish and they seem to disappear in yolked oocytes. No oil vacuoles exist, as northern anchovy eggs do not contain oil droplets.

Partially Yolked Oocytes

Oocytes in this class are in the early stages of yolk deposition (vitellogenesis) and range in size from 0.3 to 0.5 mm (major axis) (Fig. 1d, g). The class includes oocytes in the initial stage of yolk deposition up to and including those in which yolk granules or spherules extend 3/4 of the distance from the periphery to the perinuclear zone. Yolk deposition starts at the periphery of the oocyte cytoplasm as small eosinophilic staining granules and then subsequently spreads internally until it nearly reaches the finely granular perinuclear zone. Usually by this time the granules have become small spherules. The oval-shaped nucleus of oocytes in this class contains several nucleoli. At the time yolk appears in the oocyte, delicate striations appear on the hyaline membrane between the oocyte and follicle layer and it is henceforth referred to as the zona radiata. As maturation proceeds, the follicle layer becomes wider due to an increase in the width and proliferation of the granulosa cells. The thecal cells do not increase in size but remain elongated, flat cells with occasional blood capillaries, and form a thin outer covering to the follicle. The thecal cells do not change until hydration, when they become even flatter and have a stringy appearance.

Yolked Oocytes

Oocytes in this class range from 0.45 to 0.80 mm (major axis) and all contain yolk spherules or globules throughout the region between the periphery of the oocyte and the perinuclear zone (Fig. 1c, d). As vitellogenesis continues, the yolk varies from spherules in the smaller oocytes to large globules in the larger ones. Just prior to spawning (<24 h) the globules fuse to form yolk plates (Fig. 1h). Such oocytes are excluded from this class, since this characteristic is diagnostic of the last (hydrated) class of oocytes. The nucleus of oocytes in the yolked class is oval with numerous nucleoli and is centrally located until just before hydration, when it migrates to the animal pole. The granulosa cells have a wide rectangular shape in cross section and a large oval nucleus; their walls are clearly evident in sagittal section where they form polyhedrons. The zona radiata is a wide, striated, eosinophilic band until hydration, when it stretches thin and the striations seem to disappear.

Hydrated Oocytes

These oocytes range in size from 0.75 to 1.2 mm (major axis) (Fig. 1g, h). Hydration (rapid uptake of fluid by the follicle; Fulton 1898) begins at about the time the nucleus has completed its migration to the animal pole (Fig. 1e, f) and yolk globules have begun to fuse, forming yolk plates. The nucleus of a hydrated oocyte is not visible because after the nucleus has arrived at the animal pole the nuclear membrane disintegrates, dispersing its contents into the cytoplasm. During hydration, all yolk globules fuse into plates and the oocyte expands greatly, stretching the granulosa and thecal cell layers. At this time the granulosa cells in cross section appear as long, thin rectangles, the thecal cells are extremely flat and have a string-like appearance, and the zona radiata is very thin and lacks striations. Hydrated oocytes are the most ephemeral of all oocyte classes since this stage lasts for less than a day, whereas the other stages are always present in reproductively active anchovy ovaries. Migratory nuclei may be seen as early as 24 h before ovulation, but hydrated oocytes in which all globules are fused to form yolk plates do not occur earlier than 12 h before spawning. We have observed no atresia in hydrated oocytes; apparently, in northern anchovy, nearly all hydrated oocytes are ovulated.

The hydrated oocyte stage in northern anchovy begins when the nuclear membrane disintegrates and ends at ovulation. As this was an arbitrary decision, the duration of this stage could be increased by including the period of nuclear migration. This broader definition of the hydrated stage might be useful when sampling occurs before complete hydration or if hydration occurs very rapidly, as might be the case in tropical fishes.

ESTIMATION OF SPAWNING FREQUENCY

Postovulatory Follicle Method

In northern anchovy, each hydrated oocyte is surrounded by a thinly stretched follicle of an inner, epithelial layer of granulosa cells and a single, outer connective tissue layer of thecal cells with some blood capillaries. At ovulation, the fully hydrated oocytes are released from their encompassing follicles. The follicle does not fragment and pass out of the ovary with the hydrated oocyte but retains its integrity. The follicle collapses away from the opening formed for the release of the hydrated oocyte into the lumen and remains in the ovary as an evacuated follicle, or postovulatory follicle. Spawning occurs simultaneously with ovulation or in <60 min after ovulation. Initially, the postovulatory follicle is a distinct structure, but it rapidly deteriorates and is resorbed. In northern anchovy, by 48 h after ovulation postovulatory follicles can no longer be accurately discriminated from the intermediate stages of atretic oocytes.

To use postovulatory follicles for estimation of spawning frequency, it is necessary to divide the deterioration and resorptive processes of the follicle into a series of distinct histological stages, each with an assigned age (time from spawning). This requires a series of ovary samples taken at regular intervals from the time of spawning and can be accomplished by spawning fish in the laboratory (Leong 1971)

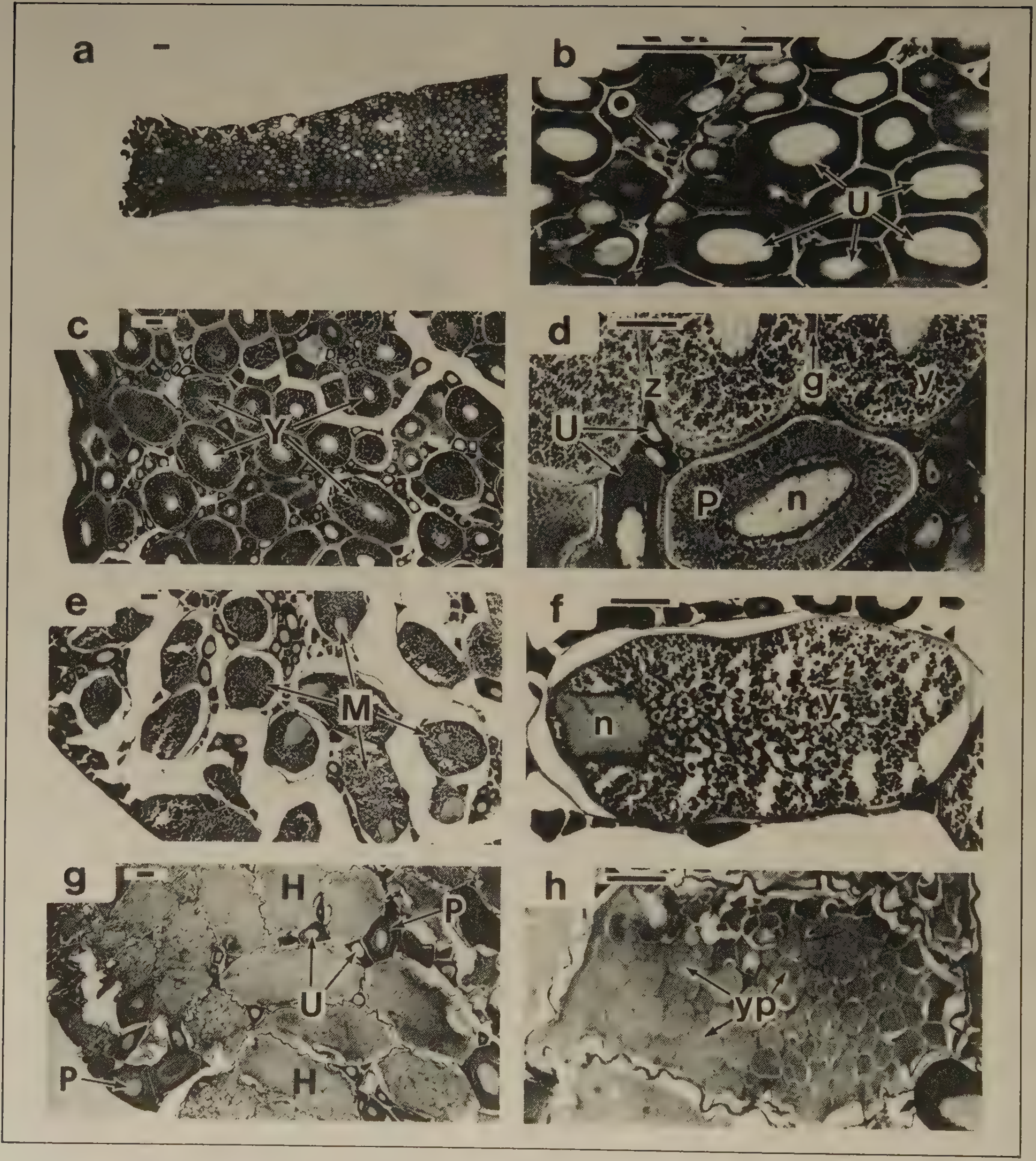

Figure 1.—Development of northern anchovy ovary at various magnifications. Stain = H&E; bar = 0.1 mm.

a) Immature ovary consisting of unyolked oocytes and no atresia.

b) Enlargement of (a) showing small, spherical, unyolked oocytes (U) with a large central nucleus and "oogonium nests" (o).

c) Normal, mature ovary with many fully yolked oocytes (Y).

d) All stages of oocytes: unyolked (U), partially yolked (P), and yolked (Y), are present in normal mature ovaries. (g = granulosa epithelial cell layer; z = zona radiata; n = nucleus; y = yolk globules.)

e) Prespawning ovary showing oocytes in the migratory nucleus stage (M).

f) Enlargement of a migratory nucleus oocyte (M). (n = nucleus; y = yolk globules.)

g) Imminent (<12 h) spawning ovary with hydrated oocytes (H) still within their follicle layers. (U = unyolked; P = partially yolked.)

h) Enlargement of a hydrated oocyte. Note that the yolk globules have fused into yolk plates (yp), and there is no prominent nucleus due to disintegration of the nuclear membrane.

or by sampling spawning schools over a 24-h period in the sea (Goldberg et al. 1984; Alheit et al. 1984). The latter approach requires estimating the average time of spawning for the population and has somewhat greater uncertainties than the preferable laboratory approach. At moderate temperatures (~16°C) we recommend taking samples of at least 10 females with postovulatory follicles at 4-h intervals for 3-4 d. At higher spawning temperatures, e.g., 28-30°C, sampling at 1-2 h intervals might be required. Once the classification criteria and stages are defined, it is necessary to conduct a blind classification of ovaries that include females with all stages of postovulatory follicles as well as those without these structures. The classification system we employ for northern anchovy is described below, and the results of the original blind classification are given in Hunter and Goldberg (1980), although our level of accuracy has considerably improved since that initial test.

Age "0 Day" postovulatory follicles in anchovy—Included in age 0-day postovulatory follicles are those new, remnant, evacuated follicles that are from 0 to 23 h old. In our surveys, however, we include in this age those postovulatory follicles about 0 to 5 h old since we trawl for northern anchovy only during the nightly spawning period (1800-0300 h). In laboratory-spawned females sacrificed 0-4 h after spawning, the new postovulatory follicles show no signs of degeneration but they may undergo some structural changes. At ovulation, while the follicle is collapsing, the follicle cell layers, appearing cord-like, form loose folds or loops. The granulosa cells, which had been extensively stretched during hydration, appear elongated and narrow with a large prominent nucleus in the center (Fig. 2a); the thinly stretched thecal layer thickens and becomes more noticeable. After spawning, the fully collapsed postovulatory follicle is a much more tightly folded or looped structure. It is relatively large, irregular in shape, with an irregular lumen which frequently contains eosinophilic granules of uncertain origin. The granulosa cells of this new postovulatory follicle (age-0 day) are characteristically columnar or cuboidal and in some cases have hypertrophied slightly; these cells are arranged orderly along the edge of the lumen with their cell walls usually evident and possessing prominent nuclei. The nucleus of the granulosa cells may be located at either the apex or base of the cell. In field-caught fish, the follicles with apical nuclei appear to occur in fish taken near the time of spawning and those having basal nuclei somewhat later (Fig. 2b, c). After spawning, the thecal cell layer is more clearly defined, adheres closely to the granulosa layer, and contains blood capillaries.

We use the above characteristics of the follicle plus no signs of follicle degeneration as the diagnostic characteristics of postovulatory follicles of age 0-day. Our surveys occur only at about the time of spawning, about 1800 to 0300 h, an insufficient period for significant follicle degeneration to occur. If sampling times were extended 6-8 h or longer after the peak hour of spawning, early degenerative follicle characteristics would have to be included as a characteristic of age 0-day postovulatory follicles. Degeneration appears to start 6-8 h after spawning in northern anchovy. The first sign of degeneration is the presence of a few pycnotic nuclei in the granulosa cells, followed shortly by the migration of a few lymphocytes into the postovulatory follicle; finally a few vacuoles appear in the granulosa layer. In northern anchovy, all of these events occur before the postovulatory follicle is 12 h old.

Age "1 Day" postovulatory follicles in anchovy—Degeneration is pronounced in postovulatory follicles examined about 24 h after spawning. The characters we use to classify postovulatory follicles as age 1-day are those that appear between 19 and 28 h after spawning, since our surveys occur only near the time of spawning. We describe follicles of age 19-28 h and subsequently discuss identification of older follicles.

By 19-28 h after spawning, the regressing postovulatory follicle is greatly shrunken and has fewer folds, hence a less irregular form than a new postovulatory follicle. The lumen, which is much reduced, may contain some granular material, although not as much as occurs in the lumen of 0-day postovulatory follicles. The granulosa cells of the follicle no longer have the orderly alignment characteristics of age 0-day postovulatory follicles, although some pattern in arrangement of cells can still be seen. Some of the nuclei of the granulosa cells are pycnotic, vacuoles are common, and only few of the cell walls are intact. The underlying layer of thecal cells is present, although less distinct, than in an age 0-day postovulatory follicle (Fig. 3).

Postovulatory follicles older than 28 h in anchovy—Classification beyond 28 h becomes difficult as the follicle continues to degenerate, and by 48 h it may easily be confused with the beta stage of atretic follicles (see section on atresia). A postovulatory follicle 48 h old is one-half to one-fourth the size of 24-h-old follicles, the lumen is much reduced or absent, and no eosinophilic granules are present. Cell walls are absent in the remaining granulosa layer tissue, and a few vacuoles or pycnotic nuclei may be seen. The theca is present but is often indistinct as it becomes incorporated into the ovarian connective tissue stroma. The number of postovulatory follicles in the ovary appears to be reduced by 48 h after spawning. Fewer follicles may be present because they were resorbed or, alternatively, fewer may be seen per section because of the growth of the larger oocytes. We believe that by 3-4 d after spawning all postovulatory follicles have been resorbed, although they might produce a structure that is indistinguishable from delta-stage atretic follicles. However, delta-stage atretic follicles are far less numerous in the ovary than new postovulatory follicles.

Postovulatory follicles in other fishes—The structure of ovaries among teleosts is relatively similar to anchovy especially in species that spawn unadorned pelagic eggs. As far as we can ascertain, the postovulatory follicles of such fishes differ only in minor details from the descriptions we have provided for the northern anchovy. The postovulatory follicles of the Peruvian anchovy, *Engraulis ringens*, is identical in all respects to that of the northern anchovy, regardless of follicle age, and hence will not be discussed further. We illustrate and briefly describe postovulatory follicles of four other species to indicate the variation in these structures among common commercial fishes that spawn unadorned pelagic eggs of about 1 mm diam. These fishes include Pacific sardine, *Sardinops sagax*, Chilean hake, *Merluccius gayi*, chub mackerel, *Scomber japonicus*, and black skipjack, *Euthynnus lineatus*.

The new postovulatory follicle (near the time of spawning) of these four species has the following characteristics in common with northern anchovy: a very convoluted shape with many folds or loops; a lumen containing some granular or particulate material; a definite granulosa epithelial cell layer lining the lumen; linearly arranged granulosa cells of cuboidal or columnar shape which contain a prominent nucleus; a definite thecal connective tissue layer with blood capillaries; and, most importantly, no degeneration of the follicle. Various minor differences from anchovy in the appearance of a new postovulatory follicle are mentioned below. The new postovulatory follicles of chub mackerel seem to differ from anchovy only in the presence of fewer granules in the lumen just after spawning (Fig. 4a, b). In the Chilean hake, the granulosa layer at the time of spawn-

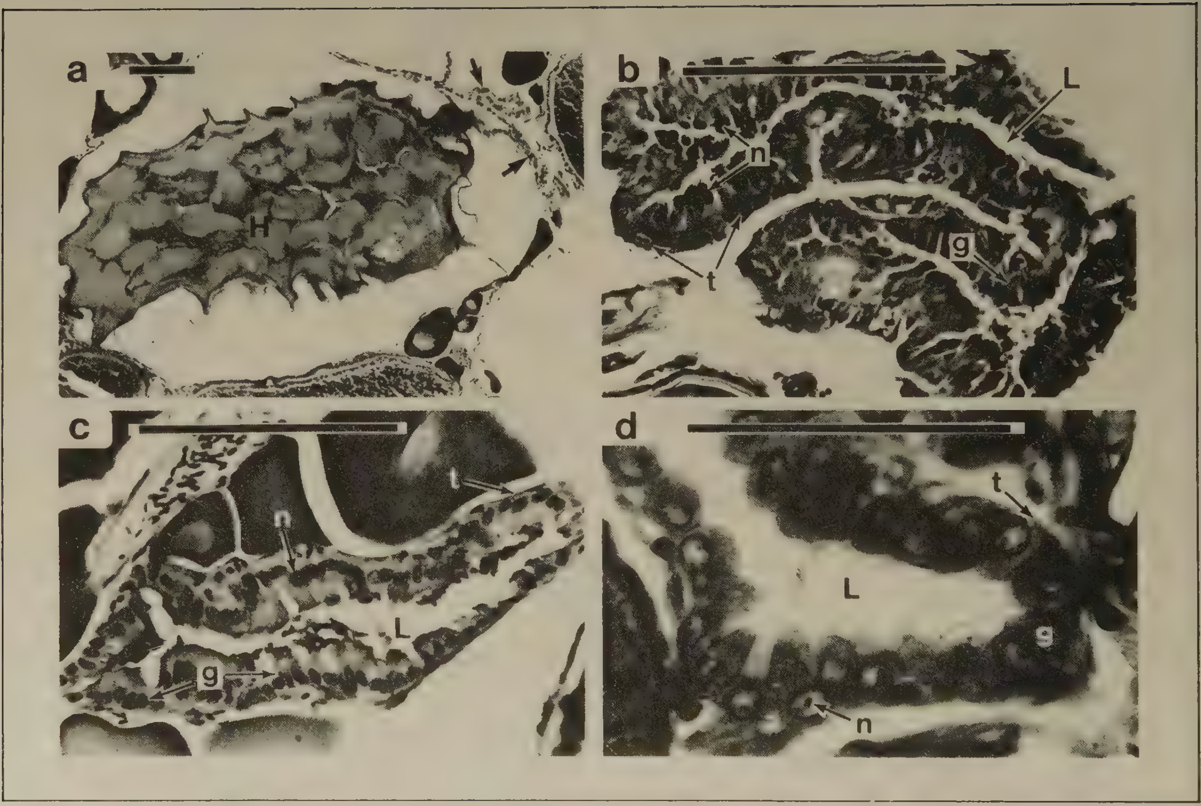

Figure 2.—Postovulatory follicles of age 0-day; elapsed time from spawning about 0-6 h. In a, b, and c, bar = 0.1 mm; in d, bar = 0.05 mm; g = granulosa epithelial cell layer; t = thecal connective cell layer; and L = lumen of follicle.

a) At ovulation the postovulatory follicle (arrow) collapses away from the hydrated oocyte (H).

c) Follicle with the nuclei (n) at the base of the granulosa cells (g). Elapsed time from spawning is 1-6 h.

b) Newly collapsed follicle with nuclei (n) at the apex of the granulosa cells (g). Elapsed time from ovulation <1 h.

d) Enlargement of follicle age 0-day (from Hunter and Goldberg 1980).

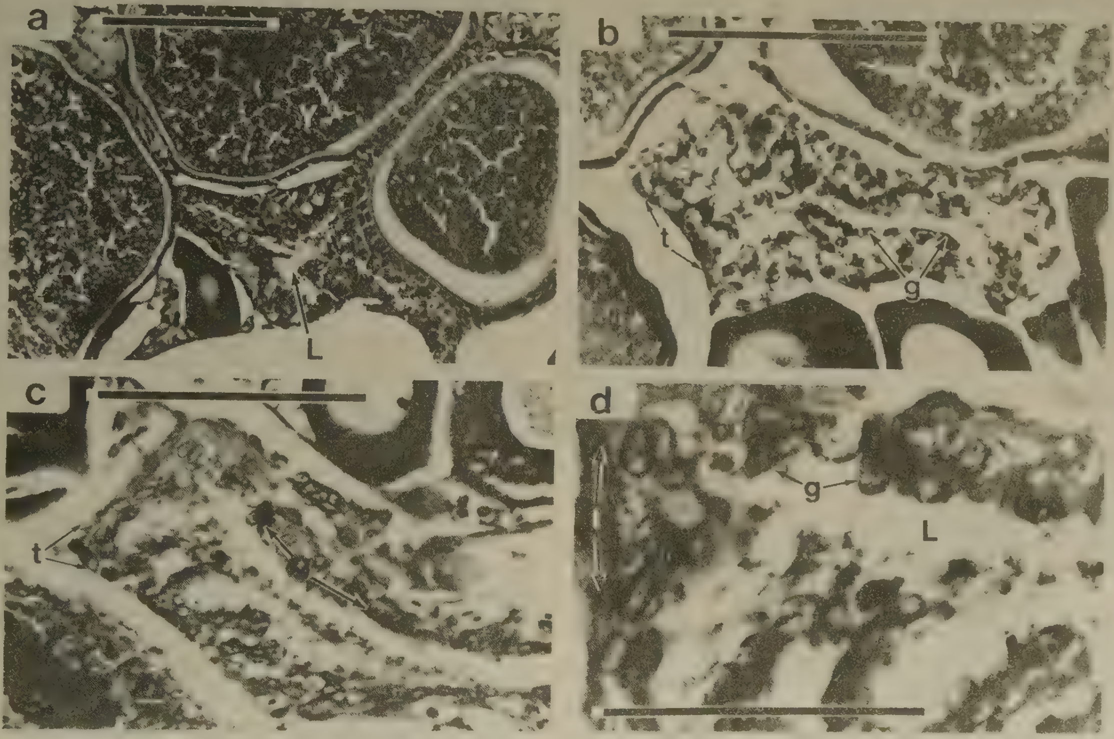

Figure 3.—Postovulatory follicles of age 1-day; elapsed time from spawning about 24 h. Degeneration of the follicle is pronounced by 24 h. In a, b, and c, bar = 0.1 mm; in d, bar = 0.05 mm; g = granulosa epithelial cell layer; t = thecal connective cell layer; L = lumen of follicle.

a, b) Follicles from sea-caught anchovies; the next batch of yolked oocytes (Y) is evident.

c, d) Follicle from anchovy spawned in the laboratory (from Hunter and Goldberg 1980).

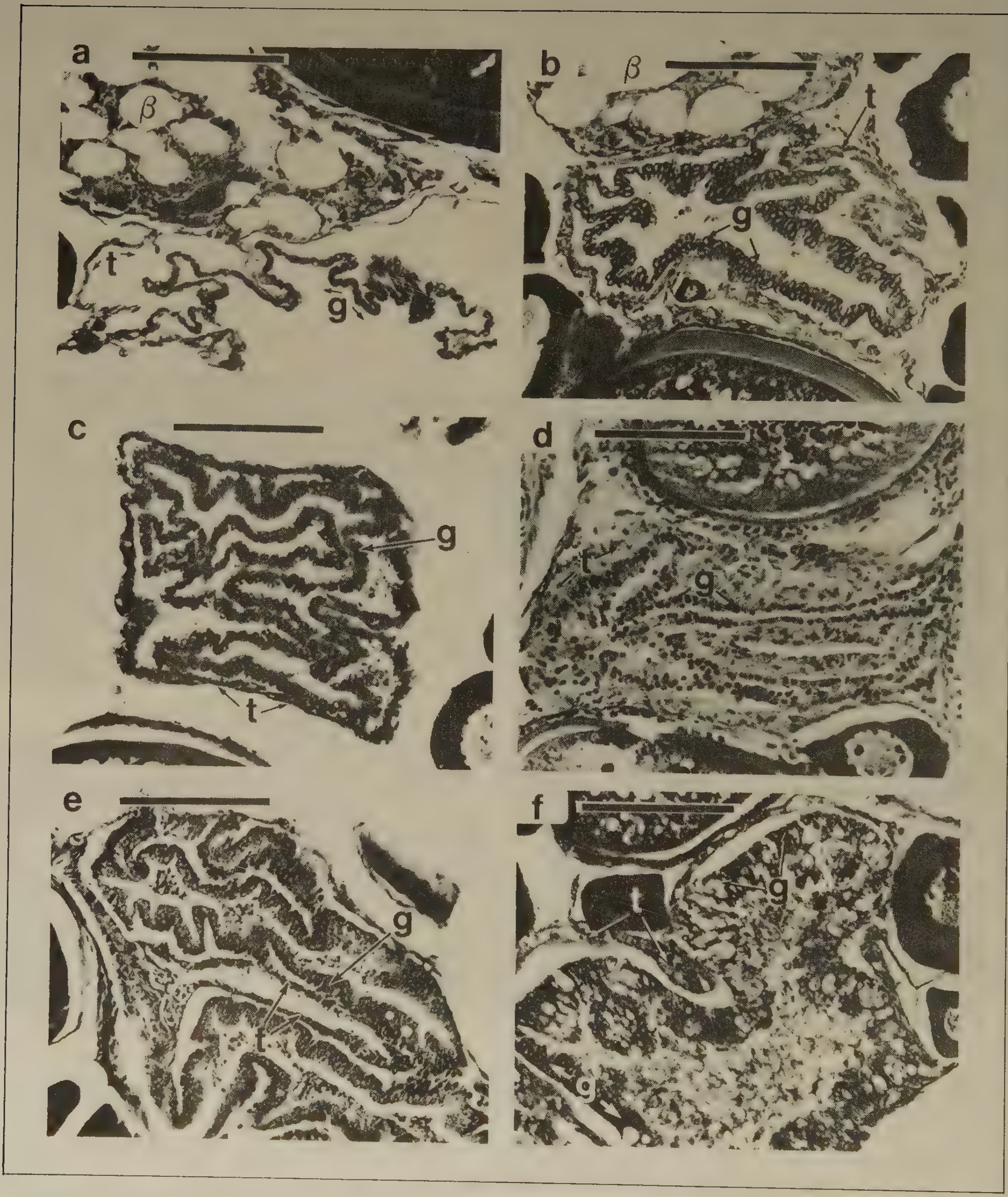

Figure 4.—New postovulatory follicles of four species of marine fishes. Bars = 0.1 mm; β = beta atresia; g = granulosa epithelial cell layer; t = thecal connective cell layer.

a) Chub mackerel, *Scomber japonicus*, at ovulation, and

b) 1 h after spawning (laboratory-induced with hormones). In both sections (a) and (b), a single beta-stage atretic follicle (β) is present; in (a), the atretic follicle contains 12-13 vacuolated areas which may be remnants of the oil droplet.

c) Chilean hake, *Merluccius gayi*. Histological material from S. R. Goldberg, Whittier College, Whittier, CA.

d) Black skipjack, *Euthynnus lineatus*, at the time of spawning (hydrated oocytes were in lumen of the ovary). Histological material from K. Schaefer, IATTC, La Jolla, CA.

e) Pacific sardine, *Sardinops sagax*, from Peru after spawning at sea. Histological material from S. R. Goldberg, Whittier College, Whittier, CA.

f) At ovulation (laboratory-induced with hormones).

ing appears to be coiled up inside a less irregular thecal layer covering, and the lumen is less distinct than anchovy and contains many fewer granules (Fig. 4c). The follicles of black skipjack differ from anchovy only by the presence of a thicker thecal layer that adheres to the granulosa cells (Fig. 4d). The only differences between sardine (Goldberg et al. 1984) and anchovy in the appearance of new postovulatory follicles are the slightly longer columnar granulosa cells, the occurrence of more particles in the lumen, and a few vacuoles in the granulosa cells of the sardine (Fig. 4e). During ovulation the sardine follicle may have quite a different appearance from the anchovy as the granulosa layer contains numerous vacuoles and the cells are more strongly hypertrophic (Fig. 4f). These differences in the appearance of new postovulatory follicles seem trivial relative to their overall similarities, indicating that the new postovulatory follicles of most fishes should be easy to identify using the general characteristics we have described.

We now consider the characteristics of degenerating postovulatory follicles in these four species and how they compare to the descriptions for the northern anchovy. The four species have the following characteristics in common with anchovy: an irregular shape that is smaller and much less convoluted than a new postovulatory follicle; the presence of a lumen, although the size may be greatly reduced; degeneration of granulosa cells (pycnotic nuclei, few cell walls, vacuoles usually present, and lack of alignment of nuclei); and an identifiable thecal layer. The degenerating postovulatory follicle (about 24 h old) of chub mackerel differs from the anchovy because a few red blood cells may occur among the granulosa cells and in the lumen and because very few vacuoles occur in the granulosa layer (Fig. 5a). Bara (1960) noticed red blood cells in the lumen of a degenerating postovulatory follicle of the Atlantic mackerel, *Scomber scombrus*, indicating this may be a common characteristic of *Scomber*. In the degenerating postovulatory follicles of the Chilean hake, some of the pycnotic granulosa cells appeared to have been sloughed into the lumen, a characteristic not seen in anchovy ovaries, and the granulosa cells contained very few vacuoles relative to the anchovy (Fig. 5b). In addition, the thecal layer in the hake now appears to be in closer contact with the remaining granulosa layer than it is in a new postovulatory follicle. The degenerating follicles in black skipjack differ from anchovy by the presence of a much thicker thecal layer surrounding the granulosa layer (Fig. 5c). The degenerating follicle of the sardine (age about 24 h) differs from the anchovy and from a new sardine postovulatory follicle by having a considerably thicker thecal layer and by the separation of the granulosa layer from the thecal layer. In addition, the degenerating granulosa cells of the sardine may be enlarged slightly and may be sloughed into the lumen (Fig. 5d). These differences among degenerating postovulatory follicles indicate minor differences in oocyte structure and perhaps differences in the pattern of resorption among species. However, our descriptions for northern anchovy can be used as a general guide for identification of postovulatory follicles in these and presumably other species. After identification of postovulatory follicles, it is best to age them by laboratory experiments or round-the-clock sea samples (see previous section).

A cautionary note on ageing postovulatory follicles—The persistence of postovulatory follicles in the ovary of the northern anchovy and the Peruvian anchovy is the same, and it appears that Pacific sardine may have a similar duration. These species spawn at moderate temperatures, 13-19°C. In tropical species that spawn at high temperatures, spawning frequency, resorption of postovulatory follicles, and ovarian maturation all may be accelerated. For example, the dragonet, *Callionymus enneactis*, spawns daily at 28-30°C, and postovulatory follicles are not seen 15 h after spawning and were only clearly distinguishable up to 3 h after spawning (Takita et al. 1983). Clearly in such a rapidly maturing ovary, postovulatory follicles would be highly transitory in nature. Thus, the duration of postovulatory stages must be newly estimated for each species, and an assumption that the duration of these stages in a new species is similar to northern anchovy is highly speculative.

Anatomical Maturity Scales and the Gonosomatic Index

Systems for grading ovaries according to macroscopic characteristics have long been used in fishery research; they include the Hjort scale (Bowers and Holliday 1961) and numerous others (see, for example, Holden and Raitt 1974; Macer 1974; Foucher and Beamish 1977; and Robb 1982). Typically, these systems include an immature stage, several stages for maturing ovaries, one for active ovaries, 1-2 stages for hydrated ovaries ("ripe" or "running ripe"), and various stages for "spent" ovaries. At present only the hydrated oocyte stage or stages have sufficiently distinct macroscopic characteristics (large ovary size, large hyaline oocytes) to be of value for estimating spawning frequency.

The terminology used in maturity scales to identify "spent" ovaries is confusing, as "spent" may refer to ovaries with new postovulatory follicles or to atretic postspawning ovaries. Macer (1974) used the terms "spent" and "partially spent" to make this distinction. At present the anatomical stages that seem to be equivalent to postovulatory ovaries are too ambiguous to be used to estimate spawning frequency. It might be possible using a laboratory calibration to identify some macroscopic characteristics that could be used to identify postovulatory ovaries for a short time after spawning. On the other hand, hydrated ovaries and postovulatory ovaries (<24 h old) have similar sampling biases. Thus, the need to develop such anatomical criteria is not great unless postovulatory ovaries could be detected macroscopically 24 h after spawning, which seems unlikely.

The gonosomatic index (GSI)—the ratio of ovary weight divided by fish weight or the equivalent (Davies 1956)—can be used to detect hydrated ovaries since the wet weight of hydrated ovaries is two to four or more times that of other maturity stages. However, the GSI has the inherent problem that dividing by an expression of body size usually does not compensate completely ("normalize") for the effects of fish size (Davies 1956; Vlaming et al. 1982). For the same reproductive state, small fish usually have a lower GSI than do larger fish, and this effect increases with maturation of the ovary (Vlaming et al. 1982; Hunter and Goldberg 1980). In other words, ovary weight increases faster with fish length than does somatic weight. The assumption underlying the GSI is that ovary weight/fish weight relation has the same slope for different maturity stages; this is clearly not the case. Thus for accurate detection of hydrated ovaries, regression analysis or other techniques are probably preferable to the simple ratio. Gonad weight has the same ambiguities as do the maturity scales when used to detect other maturity stages. Postovulatory ovaries differ little in weight from the earlier stages of postspawning (atretic) ovaries.

In summary, the traditional methodologies for assessment of reproductive condition other than histology (anatomical maturity scales, and GSI) can be used to identify females with hydrated ovaries. The incidence of such females with hydrated ovaries might be used to provide at least a crude index of spawning frequency (see

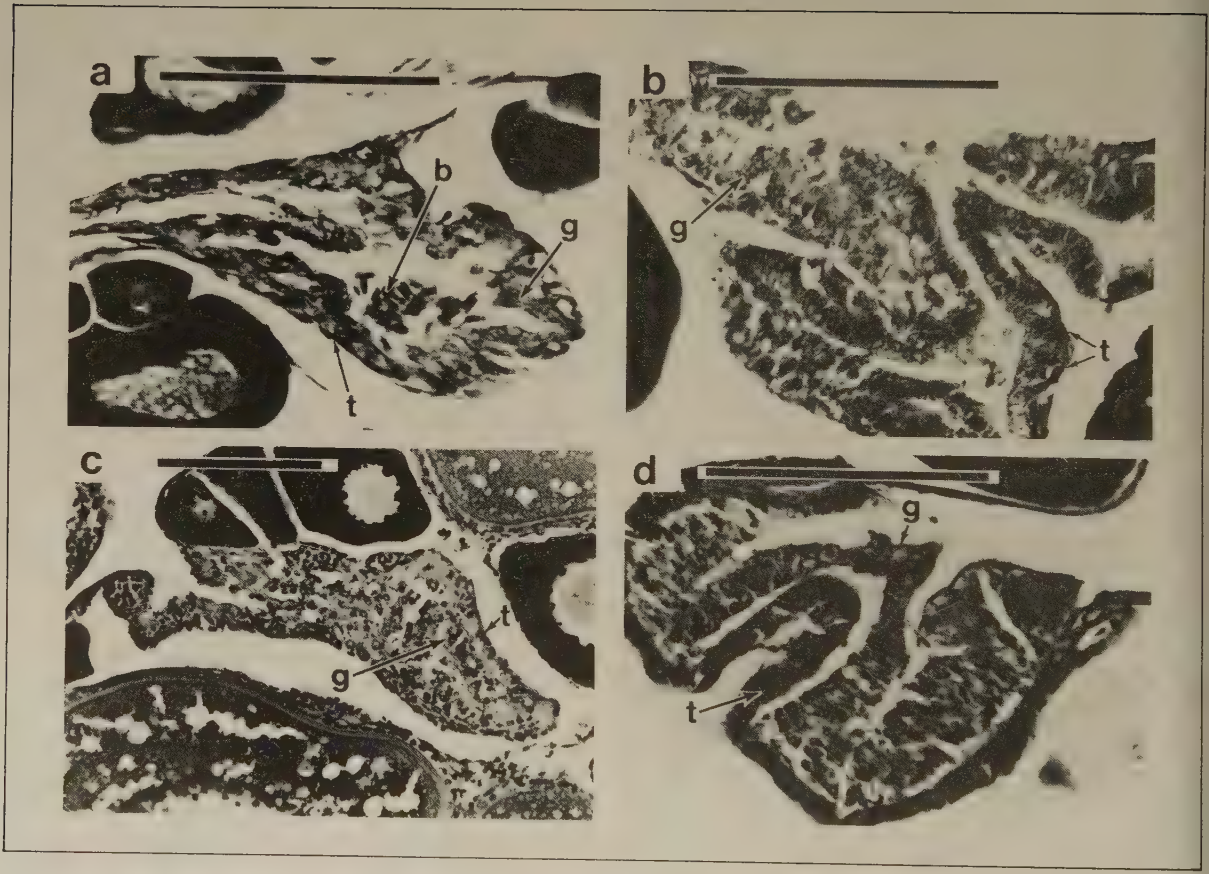

Figure 5.—Degenerating postovulatory follicles in four marine fishes. Bars = 0.1 mm; g = granulosa epithelial cell layer; t = thecal connective cell layer; b = red blood cells.

a) Chub mackerel 24 h after spawning (laboratory-induced with hormones).

b) Chilean hake. (Histological material from S. R. Goldberg, Whittier College, Whittier, CA.

c) Black skipjack. Histological material from K. Schaefer, IATTC, La Jolla, CA.

d) Pacific sardine from Peru about 24 h after spawning. Histological material from S. R. Goldberg, Whittier College, Whittier, CA.

below). These methods are useful, however, for estimating the duration of the spawning season, and they could possibly be used to provide a size or age-specific index of the relative duration of the season. At present these methodologies alone cannot be used to accurately identify in multiple spawners either postovulatory females or postspawning females, but it is possible that the GSI or maturity scale could be calibrated using histological detection of spawning frequency. Such a calibration would be worthwhile where a long historical record of GSI or maturity-scale determinations existed, because little is known of the interannual variation in spawning frequency in marine fish stocks. The technique of estimating spawning frequency using anatomical detection of females with hydrated ovaries is discussed in the next section.

Hydrated Oocyte Method

The incidence of females with hydrated oocytes can provide a quantitative estimate of the frequency of spawning in natural populations. Using this technique, DeMartini and Fountain (1981) found that the percentage of female queenfish, *Seriphus politus* (Family *Sciaenidae*), spawning per day averaged 13.6% over a 4-5 mo spawning season indicating that the mean interval between spawnings was 7.4 d. The chief advantage of the hydrated oocyte method is that spawning frequency estimates can be made using gross anatomical examinations of ovaries, and extensive histological processing and analysis are not required. Two preliminary steps required for estimation of spawning frequency using this method are outlined below.

1. **Verification of gross anatomical criteria**—The anatomical criteria used to identify hydrated ovaries must be verified using standard histological criteria, although advanced hydrated ovaries are relatively easy to identify from anatomical criteria or their weight (see Hunter et al. 1985; DeMartini and Fountain 1981). In addition, it is important to examine histologically the hydrated ovaries from females captured over the entire hydration period to determine the range of stages of hydration that are anatomically detectable.

2. **Estimation of the optimal time for sampling**—To estimate spawning frequency using the incidence of females with hydrated ovaries, females must be sampled prior to the onset of spawning, but at a time sufficiently close to the onset of spawning, so that all females destined to spawn are detectable using gross anatomical characteristics of the ovary. In addition, the duration of the period of hydration must be established and it must be documented that nearly all hydrated oocytes are spawned in less than 24 h. These determinations require that a series of samples of females be taken at regular intervals at sea over 24-48 h (see DeMartini and Fountain 1981). The optimal time for sampling females with hydrated ovaries can be determined from this series and biases caused by the onset of spawning or by the failure to detect hydration can be avoided.

The chief advantage of the hydrated ovary method over the use of the postovulatory follicles is that histological examination is not necessary after the preliminary work outlined above. On the other hand, our data on northern anchovy indicate three actual or possible disadvantages. First, sampling for the incidence of females with hydrated ovaries can be done only during a very limited portion of each day. In anchovy this period is probably 6 h or less, whereas females with day-old postovulatory follicles can be sampled at any time of day. The second possible disadvantage is that females with hydrated ovaries may be more vulnerable to trawls and perhaps other fishing gear than females in other reproductive states. This may bias an estimate based on hydrated ovaries. We find that spawning frequency estimates based on the number of female northern anchovy with hydrated ovaries and new postovulatory follicles can as much as double those estimates based on the incidence of day-old postovulatory follicles. However, this bias may be the result of the trawl oversampling the depth strata where hydrated females are abundant rather than a lack of avoidance by hydrated females. The third disadvantage of the hydrated ovary method is that incidence of females with hydrated ovaries is contagiously distributed among fish samples whereas females with day-old postovulatory follicles are not (Hunter and Goldberg 1980; DeMartini and Fountain 1981). This increases the variances of the estimate and demands a larger sample size. The contagion is probably caused by the separation of fish prior to spawning into groups composed mostly of males and hydrated females and other groups with fewer males and non-hydrated females.

Despite its actual and possible disadvantages, the simplicity of the hydrated ovary method is appealing. It seems a useful initial approach, especially since past estimates of spawning frequency were based on various speculative arguments (number of modal groups of oocytes in the ovary, or standing stock of yolked oocytes) and were in error by a factor of ten or more. The hydrated ovary method certainly provides a useful first approximation of spawing frequency at a relatively low cost.

ATRESIA

In northern anchovy, as well as in most other seasonal spawning fishes, a low incidence of oocyte atresia (degeneration of oocytes) occurs throughout the spawning season but becomes marked as the spawning season closes and the remaining advanced oocytes in the ovary are resorbed. The incidence of atresia is not used directly in the estimation of spawning biomass using the egg production method, but it is important for several other reasons: 1) A general knowledge of atresia is required to age postovulatory follicles because some stages of follicular atresia are very similar in appearance to late-stage postovulatory follicles; 2) it is a key histological marker for the cessation of spawning, and as a consequence can be used to determine whether or not a cruise period is optimal for biomass estimation (estimates near the end of the season have less precision); 3) it is necessary for accurate estimates of size at first maturity; and 4) it is essential for separating immature females from those in postspawning condition, a distinction required by the egg production method.

Atretic Stages

Oocyte degeneration or oocyte atresia has been divided into four or more sequential stages. We use the nomenclature and general characteristics defined by Bretschneider and Duyvene deWit (1947) and Lambert (1970a), but details of the descriptions of individual stages are based on our examination of northern anchovy ovaries (Hunter and Macewicz 1985).

During the initial stage of the atretic process, alpha (α), the entire oocyte is resorbed, including the yolk if present, by the hypertrophying granulosa cells of the follicle. In the second stage, beta (β), the major degeneration and resorption of the follicle (granulosa and thecal cells) occurs. In the third, gamma (γ), and fourth, delta (δ), atretic stages, regression of the theca and granulosa cells continues, greatly reducing the size of the follicle, and a yellow-brown pigment appears in H & E sections. The histological characteristics used to identify these stages in northern anchovy are outlined below.

Alpha stage atresia—In the alpha stage of atresia the oocyte is resorbed, leaving only the follicular layers. The early phase of alpha stage atresia is characterized by disintegration of the nucleus, evident by an irregular shape and granular, dark, basophilic staining, and the disintegration of some of the yolk globules, indicated by less refractive globules, fused globules, or globules expanded and of less regular shape (Fig. 6a, b, c). The zona radiata slowly dissolves as indicated by the loss of striations and uneven diameter (Fig. 6b). In the subsequent phase of alpha atresia, granulosa cells enlarge and upon rupture of the zona radiata invade the degenerating oocyte (Fig. 6d). Yolk adjacent to the invading granulosa cells liquifies (loses all structural integrity and appears as a homogeneous eosinophilic area), and becomes phagocytized by the granulosa cells as indicated by the presence of yolk in the vacuoles of these cells. The basophilic staining cytoplasm is also resorbed by the granulosa cells. In the alpha stage of atresia, blood capillaries and vessels are numerous in the thecal connective layer which does not proliferate or invade the oocyte but remains as a thin layer covering the granulosa cells. The alpha stage ends when resorption of the oocyte is complete (all cytoplasm and yolk are gone). The resulting structure (beta stage) is usually much smaller than the original oocyte. The subsequent atretic stages (beta-delta) are steps in the resorption of the remaining follicle and the structure at this point is called an atretic follicle, the term atretic oocyte being reserved for only the alpha stage of atresia.

In unyolked oocytes, the alpha stage process is similar but without yolk (Fig. 6e, f). The nucleus disintegrates, the thin pre-zona radiata (if present) dissolves, and the granulosa cells enlarge and with only a slight proliferation phagocytize the unyolked oocyte. When resorption is complete, all that remains is the atretic follicle.

Beta stage atresia—Initially the beta-stage atretic follicle is a compact structure composed of numerous disorganized granulosa cells surrounded by a thin thecal and blood vessel layer. The nucleus of some of the granulosa cells is pycnotic and many of the cells contain intracellular vacuole(s) that may be empty or contain amorphous particles. Occasionally one or more large intercellular cavities may exist among the granulosa cells (Fig. 7b, d). Preovulatory beta-stage atretic follicles containing such cavities may easily be confused with postovulatory follicles (older than 48 h), and as a consequence we do not age postovulatory follicles older than 48 h (Hunter and Goldberg 1980). In addition, small (older) beta-stage atretic follicles from yolked oocytes (Fig. 7c, d) are indistinguishable from beta-stage atretic follicles from unyolked oocytes. Thus, we do not identify the original oocyte type undergoing atresia in beta or subsequent atretic stages; such distinctions are made only for alpha-stage atretic oocytes.

Three different patterns of atresia may occur at the conclusion of the beta stage: 1) The follicle may follow the classic pattern outlined by Bretschneider and Duyvene deWit (1947) and pass through subsequent gamma and delta stages (both characterized by increased pigmentation, see below); 2) the follicle may be completely resorbed during the beta stage, leaving no histological characteristics that can be identified; and 3) the follicle may pass directly from a beta stage structure to a delta structure without passing through the intervening gamma stage. In northern anchovy, either the duration of the gamma stage is very short or few follicles pass through the gamma stage into the delta stage, because in regressing ovaries the incidence of gamma stages is very low compared to those of either beta or delta stages.

Gamma stage atresia—The gamma-stage atretic follicle is usually much smaller than the typical beta stage follicle (Fig. 7e). The granulosa cells contain flocculent material of light-yellow hue, and have nuclei of very irregular shape. The granulosa cells are surrounded by many fewer thecal cells and blood vessels than occur in the beta-stage atretic follicles. Occasionally we see an atretic follicle of quite different appearance in anchovy ovaries which we classify as a gamma-stage atretic follicle; they are included in the gamma stage because they also contain flocculent material of light-yellow hue. In this case, the flocculent yellow material is extracellular rather than intercellular and the material is encapsulated by a layer of granulosa and thecal cells. It is possible that the extracellular flocculent material is produced by the disintegration of granulosa cells.

Delta stage atresia—The diagnostic characteristic of this stage is the presence of a dark yellow-brown, finely granular pigment in the granulosa cells (Fig. 7f). The delta-stage atretic follicles are normally very small structures typically composed of 2-20 granulosa cells in the connective tissue stroma. Thecal cells and blood vessels no longer directly encompass the granulosa cells because they have been absorbed into the ovarian connective tissue stroma.

Atretic States

For population work it may be impractical to grade every ovary for the abundance of each of the four atretic stages. To simplify the assessment of atretic condition of the ovary, we have defined four atretic states which are based on some of the atretic stages described in the previous section. The duration of these states was estimated for anchovy in the laboratory and then assessed using starvation to trigger resorption of the ovary (Hunter and Macewicz 1985). In addition, the spawning potential of sea-caught females that were classed in these states was estimated by calculating the incidence of females with postovulatory follicles and hydrated eggs within each atretic state ($N > 5000$); their results are summarized below.

Atretic state 0—Females classed as atretic state 0 have yolked oocytes present and no alpha atresia of yolked oocytes. Beta stage atresia may be present but is not considered, as it cannot be separated with certainty from late-stage postovulatory follicles (>48 h old). Female anchovy in this state have a high potential of spawning, with spawning occurring at a frequency of every week to 10 d.

Atretic state 1—Females with yolked oocytes in which <50% of the yolked oocytes are in the alpha stage of atresia. Frequency of spawning of females classed in this state is less than half of that in females of atretic state 0. Thus, atretic state 1 is an index of a decline in spawning rate (Table 1). Females appeared to persist in this state under natural conditions for extended and probably variable periods, but the state persisted in the laboratory under induced starvation for only 5-7 d. Atretic state 1 is the most common atretic condition during peak spawning periods, and it can be used to detect differences in spawning between length classes; it appears to be a more sensitive index of differences in reproductive rate among length classes than is the incidence of postovulatory follicles (Hunter and Macewicz 1985).

Atretic state 2—Females with yolked oocytes in which ≥50% of the yolked oocytes are in the alpha stage of atresia. Females in atretic state 2 persisted for about 9 d in the laboratory, and it seems to have a similarly short duration in natural populations. It is the best measure of the absolute rates of ovary resorption in the population

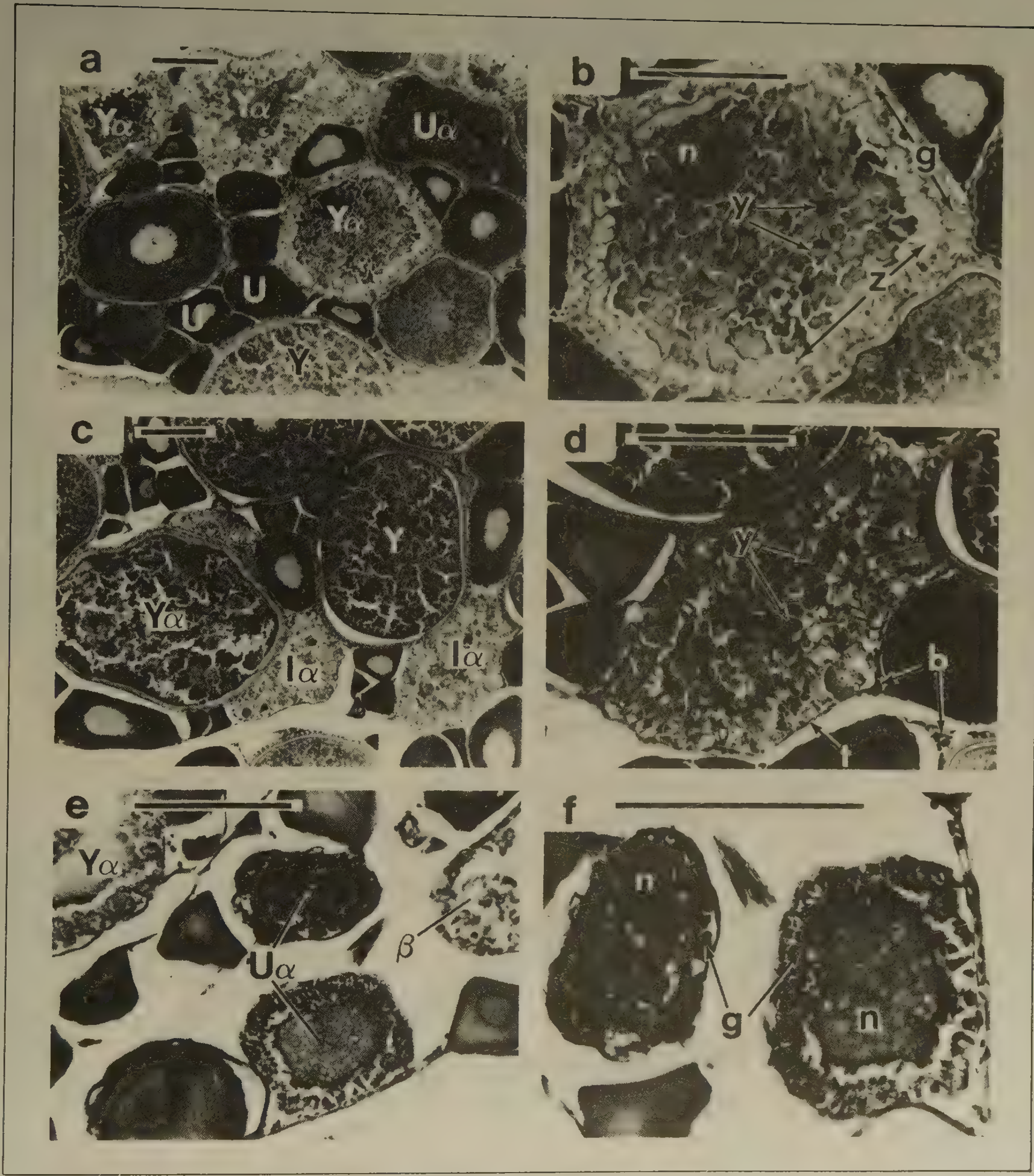

Figure 6.—Alpha (α) stage atresia in yolked (Y) and unyolked (U) oocytes. Bar = 0.1 mm.

a, b) Yolked oocyte undergoing alpha atresia (Yα). Notice dark irregular nucleus (n), uneven dissolving zona radiata (z), hypertrophic granulosa cells (g); and alpha atresia of a large unyolked oocyte (Uα).

c, d) Only remnants of yolk material (y) remain among the invasive phagocytizing granulosa cells in this late phase of alpha atresia (Iα). Note also the thecal layer (t) and the closely associated red blood cells (b). Y = yolked oocyte; Yα = alpha yolked atretic oocyte.

e, f) Unyolked oocytes in the alpha stage of atresia (Uα). Note enlargement of granulosa (g) and disintegration of nucleus (n). Yα = alpha yolked atretic oocyte; β = beta atretic follicle.

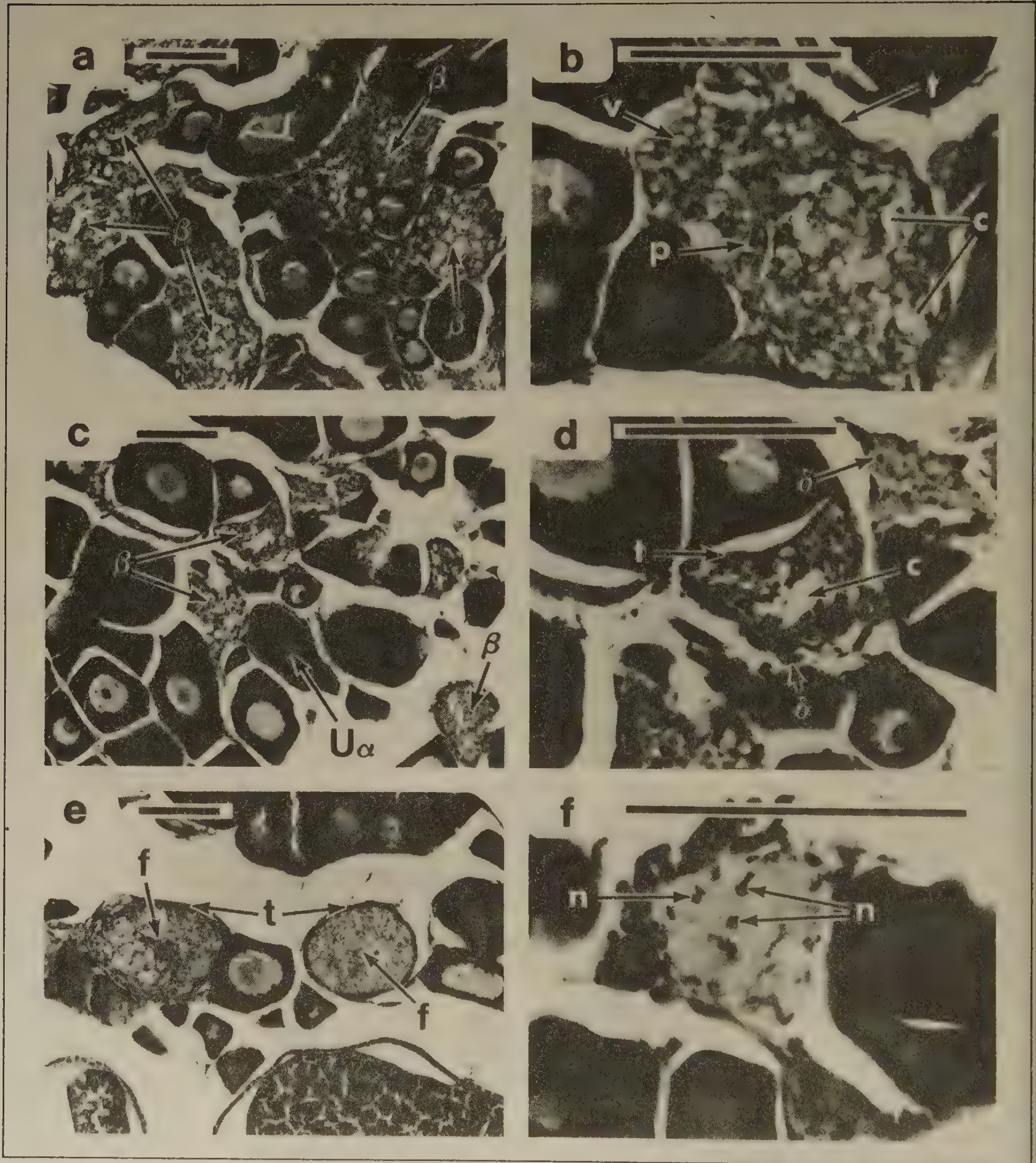

Figure 7.—Stages of atresia following complete yolk absorption. Bar = 0.1 mm.

a, b) Typical beta (β) stage atresia. Note the disorganized granulosa cells with some pycnotic nuclei (p) or intracellular vacuoles (v). t = thecal connective cell layer; c = intercellular cavities.

c, d) Disintegration of granulosa continues in these older beta (β) atretic follicles. Note the large intercellular cavity (c) and the prominent, contracted thecal cell layer (t). Also present is an unyolked oocyte in early alpha (Uα) stage and several delta (δ) stage atresia cells.

e) Two types of gamma (γ) atresia seen in northern anchovy ovaries. Note flocculent material (f) and the thecal connective cell layer (t).

f) Delta (δ) stage atresia characterized by dark-yellow, fine, granular pigment and an irregular nucleus (n).

Table 1.—Histological classifications[1] of northern anchovy ovaries and the reproductive implications. PO = postovulatory.

Ovary	State	Key histological characteristics	Reproductive implications
Spawning States			
Active	Hydrated	Hydrated oocytes present	Spawning will occur in >12 h[2]
	Age 0-day PO	Postovulatory follicles <24 h old.	Spawning occurred <24 h ago[3].
	Age 1-day PO	Postovulatory follicles 24-48 h old.	Spawning occurred 1 d ago[3].
Atretic States			
Active	0	Yolked oocytes present; no alpha-stage atretic yolked oocytes.	High probability of spawning within 1-10 d[4].
	1	Alpha stage atresia of yolked oocytes; ≥50% of yolked oocytes are affected.	Probability of spawning is half that of atretic state 0[5].
Inactive	2	Alpha stage atresia of yolked oocytes; ≥50% of yolked oocytes are affected.	Probability of spawning = 0; may have had an active ovary 1-20 d ago (average 8 d)[6].
	3	No yolked oocytes present; beta stage atresia present.	Probability of spawning = 0; may have had an active ovary ≥16-30 d ago[6].
	Immature	No yolked oocytes present; no beta atretic follicles.	Probability of spawning = 0; no evidence of past reproduction within last 30 or more d. May develop an active ovary within ≥31 d[7].

[1] Ovaries are classed into both spawning and atretic states, but the reproductive implications are for a single-state classification and not for a combination of atretic and spawning states.

[2] Hunter and Macewicz 1980.

[3] Hunter and Goldberg 1980.

[4] In peak spawning months the average female spawns at 1-10 d intervals (Hunter and Leong 1981); hence females with active ovaries are likely to spawn within 1-10 d depending on maturity of the ovary.

[5] Based on the fraction of females in spawning states within atretic state 1 (Hunter and Macewicz 1985).

[6] Hunter and Macewicz 1985.

[7] Hunter and Leong 1981.

and could be used to forecast the end of reproduction near the end of the spawning season. A high incidence of females in this state indicates that cessation of spawning in the population is imminent.

Atretic state 3—Females without yolked oocytes in which beta stage atresia is present. This state identifies females in late postspawning condition. The state persisted for about 30 d in the laboratory, and it may last much longer under natural conditions while the numerous small oocytes are resorbed. (The laboratory data indicate that the duration of this state could be increased if definitions were redefined to include gamma + delta stages of atresia which have a longer life in the ovary than does the beta stage.) This state is used to separate females in postspawning condition from immature females (females with no previous reproductive history). Consequently, identification of females in this state is essential for accurate estimates of age or size at first maturity and for an accurate definition of spawning biomass using the egg production method.

TESTING THE ASSUMPTION OF SEASONALLY DETERMINATE FECUNDITY

A critical assumption underlying some biomass estimates from ichthyoplankton data and many estimates of annual fecundity in fishes is that the annual fecundity in a species is determined at the beginning of the spawning season. Validation of this assumption of determinate fecundity requires proof that 1) all oocytes destined to be spawned in a season are identifiable at the beginning of the season and no new spawning batches are recruited from the reservoir of small unyolked oocytes that exist in the ovary the year round, and 2) the identified standing stock of yolked oocytes that constitute the maximum potential annual fecundity are in fact spawned and only a negligible quantity of these oocytes are resorbed at the end of the season.

The traditional evidence for determinate fecundity is the presence of a major gap in oocyte maturity stages or size classes between the oocytes matured for the season and the reservoir of immature oocytes present year-round in the ovary (Yamamoto 1956). The presence of such a gap in oocyte classes in females taken at the beginning of the season seems to be adequate proof that the standing stock of oocytes is a measure of maximum annual fecundity, as long as the gap is not between a batch of hydrated oocytes and other yolked oocytes. The absence of such a discontinuity in oocyte classes is evidence for indeterminate fecundity. In some cases, however, determinate annual fecundity is believed to exist despite the fact that oocyte size classes are continuously distributed in the ovary. In such cases, spawning frequency and batch fecundity for the species must be estimated over the season and their product (fecundity × frequency) compared to the standing stock of mature oocytes at the beginning of the season. This was done for whiting and haddock in the laboratory by Hislop (1975) and Hislop et al. (1978).

For northern anchovy, Hunter and Leong (1981) compared field estimates of spawning frequency with standing stocks of oocytes. They showed that oocytes as small as 0.1 mm must be included in the annual fecundity to account for 10 spawnings per yr and estimated that anchovy spawn an average of 20 or more times per yr. Their analysis clearly documents the existence of indeterminate fecundity in anchovy. However, anchovy have a continuous oocyte distribution, and so indeterminate fecundity is expected in this species.

In species for which determinate fecundity is inferred because of a discontinous oocyte distribution, it is also necessary to document that the maximum annual fecundity estimated from the standing stock of oocytes is in fact realized in the sea (see above). To validate this assumption requires an analysis of rates of atresia of yolked and partially yolked oocytes. The key atretic state in such an analysis would be one similar to our atretic state 2 where many oocytes are in the alpha stage of atresia. It should be borne in mind that this state may have a short duration.

In anchovy the mean duration of this state is only 9 d and the maximum only 20 d (Hunter amd Macewicz 1985). Consequently, sampling to determine the extent of resorption of oocytes must be done over a relatively short period near the end of the season; otherwise, significant oocyte resorption may not be detected. Substantial oocyte resorption has been observed in the Pacific hake, *Merluccius productus*, which seems to have a discontinuous oocyte distribution (Foucher and Beamish 1977). They conclude that the standing stock of yolked oocytes is very likely in excess of the number of oocytes that will be spawned, except in exceptional years.

In conclusion, an assumption of determinate fecundity requires extensive work to prove, and in some cases may be only wishful thinking. The most conservative assumption is that seasonal fecundity is indeterminate for multiple spawning fishes and that estimates of batch fecundity and spawning frequency are required. The documented cases of determinate fecundity appear to be restricted to boreal or cold temperate climates where spawning seasons are short. Thus in most of the world's oceans indeterminate fecundity and multiple spawning are the rule for epipelagic spawners, and estimates of spawning frequency are essential both for biomass estimation using ichthyoplankton data and for estimates of annual fecundity.

FUTURE APPLICATIONS OF HISTOLOGICAL CLASSIFICATION OF OVARIES

An important future application of the histological classifications we have described is the study of reproductive processes in multiple spawning fish populations. This work requires not only histological classification but sufficient laboratory calibration and analysis of sea data to be able to specify the reproductive implications and duration of each class. Sufficient data exist on northern anchovy to make a relatively accurate interpretation of the reproductive significance of each spawning and atretic state (Table 1). Reproductive state and its approximate duration can now be related to the physiological state of the female (age, size, fat content, biochemical composition, instantaneous growth rate from otoliths or RNA/DNA ratios, and environmental conditions). In this way it may now be possible to identify the factors controlling the 2-3 fold variation in batch fecundity (Hunter et al. 1985), the potentially large variation in spawning frequency and duration of the spawning season, and, most importantly, the functions regulating partitioning of energy between reproduction and growth.

LITERATURE CITED

ALHEIT, J., V. H. ALARCON, and B. J. MACEWICZ.
1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25:43-52.

BARA, G.
1960. Histological and cytological changes in the ovaries of the mackerel *Scomber scomber* L. during the annual cycle. Rev. Fac. Sci. Univ. Istanbul Ser. B. Sci. Nat. 25:49-91.

BOWERS, A. B., and F. G. T. HOLLIDAY.
1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus*, L.). Mar. Res. Dep. Agric. Fish. Scotl. 5:1-16.

BRETSCHNEIDER, L. H., and J. J. DUYVENE deWIT.
1947. Sexual endocrinology of non-mammalian vertebrates. Monographs on the progress of research in Holland during the war, Vol. II. Elsevier, N.Y., 147 p.

DAVIES, D. H.
1956. The South African pilchard (*Sardinops ocellata*) sexual maturity and reproduction 1950-54. S. Afr. Div. Sea Fish. Invest. Rep. 22, 55 p.

DeMARTINI, E. E., and R. K. FOUNTAIN.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547-560.

FOUCHER, R. P., and R. J. BEAMISH.
1977. A review of oocyte development in fishes with special reference to Pacific hake (*Merluccius productus*). Can. Fish. Mar. Serv. Tech. Rep. 755, 16 p.

FULTON, T. W.
1898. On the growth and maturation of the ovarian eggs of teleostean fishes. Annu. Rep. Fish. Board Scotl. 16:88-124.

GOLDBERG, S. R., V. H. ALARCON, and J. ALHEIT.
1984. Postovulatory follicle histology of the Pacific sardine, *Sardinops sagax*, from Peru. Fish. Bull., U.S. 82:443-445.

HISLOP, J. R. G.
1975. The breeding and growth of whiting, *Merlangius merlangus*, in captivity. J. Cons. int. Explor. Mer 36:119-127.

HISLOP, J. R. G., A. P. ROBB, and J. A. GAULD.
1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish. Biol. 13:85-98.

HOLDEN, M. J., and D. F. S. RAITT (editors).
1974. Manual of fisheries science. Part 2 - Methods of resource investigation and their application. FAO Fish. Tech. Pap. 115 (Rev.1), 241 p.

HUNTER, J. R., and S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., and R. LEONG.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

HUNTER, J. R., N. C. H. LO, and R. J. H. LEONG.
1985. Batch fecundity in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 67-77. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

HUNTER, J. R., and B. J. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency and temporal pattern in the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.
1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:119-136.

LAMBERT, J. G. D.
1970a. The ovary of the guppy, *Poecilia reticulata*. The atretic follicle, a *corpus atreticum* or *corpus luteum praeovulationis*. Z. Zellforsch. 107:54-67.

LAMBERT, J. G. D.
1970b. The ovary of the guppy, *Poecilia reticulata*. The granulosa cells as sites of steroid biosynthesis. Gen. Comp. Endocrinol. 15:464-476.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

LUNA, L. G.
1968. Manual of histological staining methods of the Armed Forces, Institute of Pathology, 3d ed. McGraw-Hill, N.Y.

MACER, C. T.
1974. The reproductive biology of the horse mackerel, *Trachurus trachurus* (L.) in the North Sea and English Channel. J. Fish. Biol. 6:415-438.

PREECE, A.
1965. A manual for histological technicians, 2d ed. Little, Brown & Co., Boston.

ROBB, A. P.
1982. Histological observations on the reproductive biology of the haddock, *Melanogrammus aeglefinus* (L.). J. Fish. Biol. 20:397-408.

TAKITA, T., T. IWAMOTO, S. KAI, and I. SOGABE.
1983. Maturation and spawning of the dragonet, *Callionymus enneactis*, in an aquarium. Jpn. J. Ichthyol. 30:221-226

VLAMING, V. de, G. GROSSMAN, and F. CHAPMAN.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31-39.

WALLACE, R. A., and K. SELMAN.
1981. Cellular and dynamic aspects of the oocyte growth in teleosts. Amer. Zool. 21:325-343.

YAMAMOTO, K.
1956. Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. 12:362-376.

RATES OF ATRESIA IN THE OVARY OF CAPTIVE AND WILD NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

J. Roe Hunter and Beverly J. Macewicz[1]

ABSTRACT

The process of ovarian atresia was described for northern anchovy using a laboratory group in which atresia was induced by starvation. Atretic characteristics of the ovary were described and illustrated, atretic ovarian states defined, and the rate that the ovary passed from one atretic stage to another was measured. The ovaries of starved females regressed rapidly; 3 days after the onset of starvation the ovaries of about half of the females contained yolked oocytes undergoing resorption of yolk (alpha stage of oocyte atresia) and by 23 days after the onset of starvation no yolk remained in the ovaries of any of the females. Gamma + delta stages of atretic follicles persisted in the ovary for over a month, but their decline in abundance indicated that eventually all signs of past reproductive activity would be lost in regressed ovaries.

In the natural population, rates of ovarian atresia increased seasonally from only a few percent of the females showing some atresia in peak spawning months to over 50% near the end of the season. Females with low levels of alpha stage atresia (<50% yolked oocytes affected) spawned about half as frequently as did those with no alpha stage atresia. Spawning was rare (1% of the females) or absent in females with high levels of alpha stage atresia (≥50% yolked oocytes affected). Late in the spawning season, it may be possible to forecast the end of spawning in the populations using the frequency of females in the populations with high levels of alpha stage oocyte atresia. Throughout the spawning season atretic rates were higher in small females (standard length ≤10 cm) than in larger ones indicating that 1-year-old females spawning for the first time have a much shorter spawning season than do older females.

Four approaches commonly used to determine the reproductive state of female fishes are 1) staging of ovaries using gross anatomical criteria such as the international Hjort scale (Bowers and Holliday 1961); 2) calculation of the gonosomatic index (GSI), i.e., gonad weight divided by female weight or the equivalent (de Vlaming et al. 1982); 3) estimating the mean diameter of the oocytes in the most advanced mode of oocytes (Hunter and Goldberg 1980; Hunter and Leong 1981); and 4) classifying ovaries histologically. Histological classification is superior to all other methods. Two of its great strengths are that the frequency of spawning of multiple spawning fish populations can be accurately estimated using the presence of postovulatory follicles (Hunter and Goldberg 1980) and that regressing ovaries can be distinguished from immature and from postovulatory ovaries. The histological criteria used to identify regressing ovaries is the presence of many oocytes and follicles undergoing resorption, a process known as atresia.

The interpretive power of histological analysis could be enhanced if the process of ovarian atresia were better documented. Specifically, ovarian atretic stages need to be defined, rates of atresia and duration of stages estimated, and the relation between ovarian atretic state and the probability of spawning determined. Such information would facilitate process oriented field studies on reproductive biology, and increase the accuracy of estimates of size at first maturity and size- or age-specific duration of the annual spawning season.

This study provides the laboratory and field calibration necessary for the assessment of the reproductive state of northern anchovy, *Engraulis mordax*, using the atretic condition of the ovary. We identify a range of ovarian atretic characteristics that define the atretic condition of the ovary, estimate rates of atresia, and estimate the duration that atretic characters persist in the ovaries of starving females in the laboratory. We use this information to classify ovaries of sea-caught females and estimate the probability of spawning for females with various levels of ovarian atresia.

We know of no similar work. A large descriptive

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literature exists on follicular atresia in fishes (reviewed by Saidapur 1978) and stages of atretic oocytes and follicles have been defined (Bretschneider and Duyvene de Wit 1947; Lambert 1970a), but only the atretic rates in the guppy have been measured (Lambert 1970a). Considerable attention has been devoted to stages of atretic follicles (corpora atretica or "preovulatory corpora lutea") because of a presumed endocrine function (see reviews by Hoar 1965; Byskov 1978). The seasonal occurrence of atretic oocytes and follicles is often discussed as part of a general description of seasonal changes in the ovary of marine fish; see, for example, cycles described for the gobiid, *Gillichthys mirabilis* (de Vlaming 1972); plaice, *Pleuronectes platessa* (Barr 1963); *Paracentropristis cabrilla* (Zanuy 1977); and three species of *Epinephelus* (Bouain and Siau 1983). The proportion of females with atretic ovaries or the numbers of atretic oocytes within the ovary is given less often, but a few reports exist. For example, atresia ranged from 0 to 6% of the oocytes in female haddock, *Melanogrammus aeglefinus* (L.) (Robb 1982); corpora atretica increased to about 3% of the oocytes during the postspawning period of the dab, *Limanda limanda* (L.) (Htun-Han 1978); and atretic oocytes varied from 13% of yolked oocytes during the prespawning period to 100% during the postspawning period of the snapper, *Chrysophrys auratus* (F.) (Crossland 1977). Some attention has been given to the issue of whether or not atretic rates can account for differences in fecundity among females fed high and low rations. It appears that ration-related differences in fecundity are more closely tied to production rates of oocytes rather than atretic rates (Tyler and Dunn 1976; Wootton 1979). In summary, our literature review indicates that ovarian atresia has yet to be used for quantitative estimation of any reproductive processes in marine fish populations, although it has been used in general descriptions of the seasonality of reproduction for many years.

METHODS

Laboratory Experiment

Adult northern anchovy captured by commercial bait fishermen on 23 February 1982 were kept in a live car in San Diego Bay. Three days later about 1,000 fish averaging 104 mm SL (9.50 g) were taken to the laboratory and held in a 4.6 m diameter pool (1 m deep) at which time the first fish sample was taken. Over the first 34 d in captivity, samples of 18-24 females were taken at 3-4 d intervals with the final sample taken after 62 d in captivity. The temperature of the seawater ranged from 15.5° to 16.5°C.

The fish were not fed during the first 27 d in captivity because starvation was used to trigger the resorption of the ovary; thereafter they were fed daily. On the 27th day of starvation the ovaries had regressed from 4% of female body weight to 0.8% and feeding was resumed because we wished to learn how long the atretic characters would last once the fish began to feed.

In our calculations of atretic rates of laboratory females, we assumed that all the females at the time of capture had active ovaries without atresia, although no samples were taken until 3 d after the fish were captured. Only 3% of the 1,680 females taken in a survey conducted at the same time (28 January-8 March 1982) had atretic ovaries, and it was prominent in only 0.1% of the females (50% or more of yolked oocytes were affected). Ninety-six percent of the females in our first sample (taken 3 d after capture) had yolked eggs, and half of them had no atresia.

All females sampled during the course of the laboratory experiment were weighed and measured, and the ovary removed, weighed, and a section removed for histological analysis. Ovaries were fixed in 10% neutral buffered Formalin[2] and embedded in Paraplast. Histological sections were cut at 6 μm and stained with Harris hematoxylin followed by eosin counterstain.

Sea Data

The ovaries of northern anchovy taken in trawl surveys used for biomass estimation (Stauffer and Picquelle[3]) and various other collections from commercial seiners and midwater trawls were histologically examined. The number of females examined per catch (trawl, purse seine, or lampara net) has varied from 10 to 20. Some collections were quite small, especially those taken outside the main spawning season in the Southern California Bight; these small collections may consist of only two catches, whereas those taken during the main spawning months (February-March) were large, often consisting of 100 or more catches of 10-20 females each. In all collections ovaries were classed according to atretic characteristics as well as on the basis of the presence of postovulatory follicles (age 0 and age 1 d) and hydrated eggs according to the method described by Hunter and Goldberg (1980). All but two of the collections were from the Southern California Bight or northern Baja California, the region where the Central subpopulation of the northern anchovy is concentrated (Vrooman et al. 1981). Two collections were from the vicinity of Monterey and San Francisco Bays. Fish from these areas appear to have a different spawning season from those of fish to the south so they are listed separately in our seasonal tabulations. All collections were classified using histological criteria to determine the incidence of ovarian atretic states as a function of female size, season, and reproductive state.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] Stauffer, G., and S. Picquelle. The 1980 and 1981 egg production estimates of anchovy spawning biomass. Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Histological Characteristics

We describe below the histological characteristics of four oocyte classes and four stages of atresia in the northern anchovy. These stages and classes are subsequently used to define various ovarian atretic states in laboratory and sea-caught female anchovy.

Oocyte Classes

The northern anchovy is a multiple spawning fish (Hunter and Goldberg 1980) with asynchronous oocyte development (oocytes in many stages of development occurring simultaneously in reproductively active ovaries; Wallace and Selman 1981). During the spawning season oocyte development is a continuous process involving all stages with a new spawning batch maturing every week to 10 d (Hunter and Leong 1981). Oocyte development and maturation in teleosts, reviewed recently by Wallace and Selman (1981), has frequently been subdivided into many stages (Andrews 1931[4]; Yamamoto 1956; Lambert 1970b), but our work required a simpler histological classification system. We have combined the stages of past authors into four oocyte classes (unyolked oocytes, partially yolked oocytes, yolked oocytes, and hydrated oocytes), and we describe the histological characteristics of each class below.

1) Unyolked Oocytes—This class includes all oocytes without yolk that are about 0.04 mm or larger and range upward in size to about 0.35 mm (U, Fig. 1a, b). Oocytes <0.04 mm are excluded because they consist mostly of "oogonium nests", do not have a true follicle layer, and do not seem to undergo degeneration (o, Fig. 1b). The smaller oocytes within this class (0.04-0.15 mm) are spherical, have a large nucleus with a narrow homogenous very densely staining cytoplasm (Fig. 1b). A very thin single layer of elongated, spindlelike cells (the beginning of the granulosa layer) surrounds these small oocytes. The large oocytes in this class are oval, the cytoplasm stains faintly with hematoxylin and has a cloudy, mottled appearance (Fig. 1d). The oval nucleus of these oocytes contains several nucleoli and is surrounded by a granular perinuclear zone. In these larger oocytes a thin, definite, faintly eosinophilic staining, hyaline membrane (precursor of the zona radiata) appears between the oocyte and the growing follicle. The follicle consists of a narrow single inner layer of cuboidal granulosa cells and a single outer layer of flat elongated thecal cells with some blood capillaries. The larger oocytes also may have some small vesicles in the periphery of the cytoplasm. These vesicles are at times difficult to distinguish and they seem to disappear in yolked oocytes. No oil vacuoles exist as northern anchovy eggs do not contain oil droplets.

2) Partially Yolked Oocytes—Oocytes in this class are in the early stages of yolk deposition (vitellogenesis) and range in size from 0.3 to 0.5 mm (major axis) (P, Fig. 1d, g). The class includes oocytes in the initial stage of yolk deposition up to and including those in which yolk granules or spherules extend three-fourths of the distance from the periphery to the perinuclear zone. Yolk deposition starts at the periphery of the oocyte cytoplasm as small eosinophilic staining granules and then subsequently spreads internally until they nearly reach the finely granular perinuclear zone. Usually by this time the granules have become small spherules. The oval-shaped nucleus of oocytes in this class contains several nucleoli. Delicate striations appear on the hyaline membrane between the oocyte and follicle layer at the time yolk appears in the oocyte. As maturation proceeds, the follicle layer becomes wider due to an increase in the width and proliferation of granulosa cells. The thecal cells do not increase in size but remain elongated, flat cells with occasional blood capillaries and form a thin outer cov-

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[4] Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. manuscr., 88 p. Stanford Univ., Stanford, CA 94305.

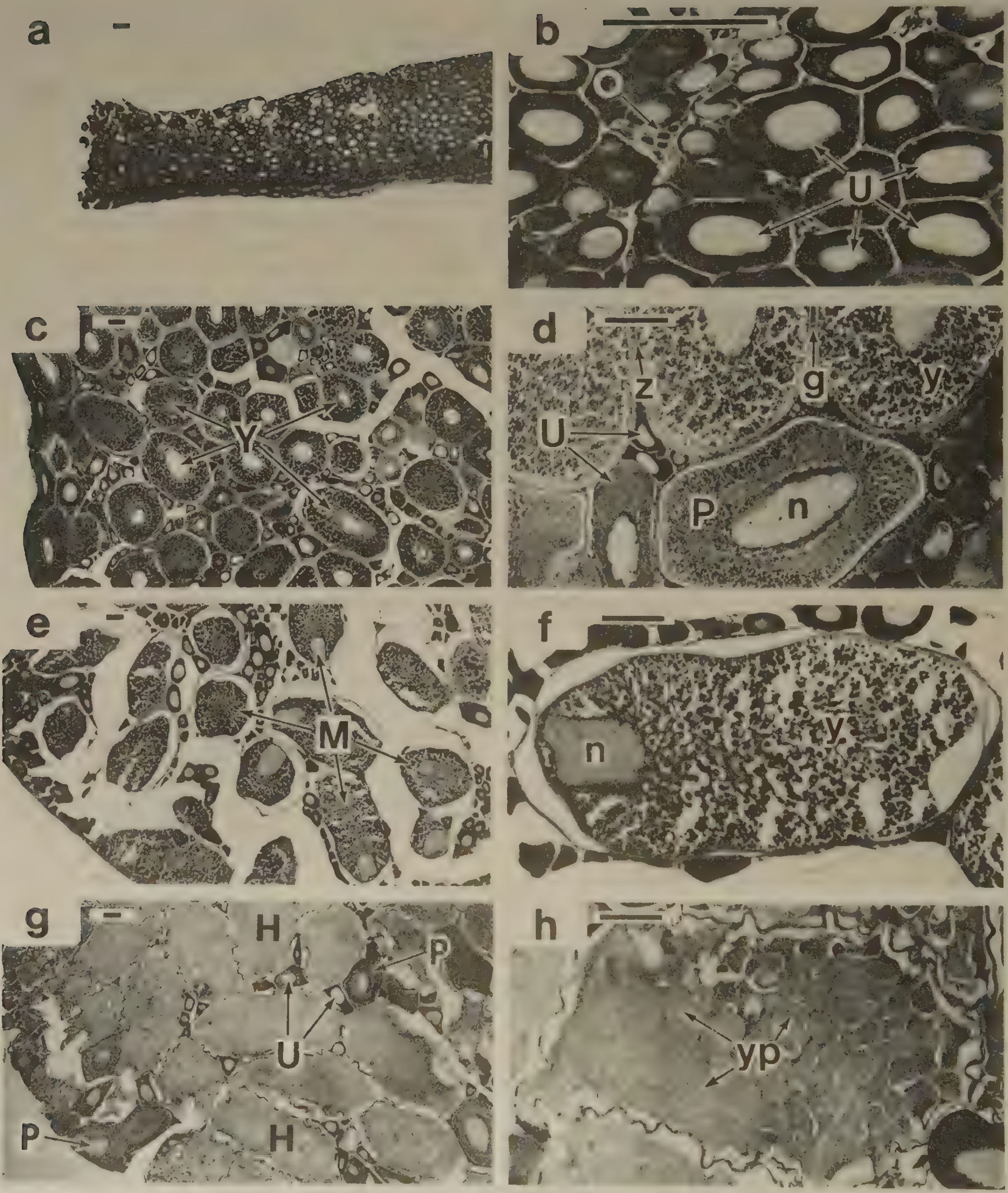

FIGURE 1.—Development of northern anchovy ovary at various magnifications (stain = H & E, bar = 0.1 mm). a) Immature ovary consisting of unyolked oocytes and no atresia. b) Enlargement of (a) showing small spherical unyolked oocytes (U) with a large central nucleus and "oogonium nests" (o). c) Normal mature ovary with many fully yolked oocytes (Y). d) All stages of oocytes, unyolked (U), partial yolked (P), and yolked (Y), are present in normal mature ovaries (g = granulosa cell layer, z = zona radiata, n = nucleus, y = yolked globules). e) Prespawning ovary showing migration of nucleus to the animal pole. f) Enlargement of a migratory nucleus oocyte (M). (n = nucleus, y = yolk globules.) g) Imminent (<12 h) spawning ovary with hydrated oocytes (H) still within the follicle layer. (U = unyolked, P = partial yolked.) h) Enlargement of a hydrated oocyte. Note that the yolk globules have fused into yolk plates (yp) and there is no prominent nucleus due to disintegration of the nuclear membrane.

ering to the follicle. The thecal cells do not change until hydration when they become even flatter and have a stringy appearance.

3) Yolked Oocytes—Oocytes in this class range from 0.45 to 0.80 mm (major axis), and all contain yolk spherules or globules throughout the region between the periphery of the oocyte and the perinuclear zone (Y, Fig. 1c, d). As vitellogenesis continues, the yolk varies from spherules in the smaller oocytes to large globules in the larger ones. Just prior to spawning (<24 h) the globules fuse to form yolk plates (Fig. 1h). Such oocytes are excluded from this oocyte class, this characteristic being diagnostic of the last class (hydrated oocytes). The nucleus of oocytes in the yolked oocyte class is oval with numerous nucleoli. The granulosa cells have a wide rectangular shape in cross section and a large oval nucleus; their walls are clearly evident in sagittal section where they form polyhedrons. The zona radiata is a wide, striated, eosinophilic band until hydration when it stretches thin and the striations disappear.

4) Hydrated Oocytes—These oocytes range in size from 0.75 to 1.2 mm (major axis) (H, Fig. 1g, h). (Hydration (rapid uptake of fluid by the follicle, Fulton 1898) begins when the nucleus has migrated to the animal pole (M, Fig. 1e, f) and yolk globules first fuse to form yolk plates, and it ends when the hydrated oocyte is ovulated. The nucleus of hydrated oocytes is not visible except in the earliest phase because after the nucleus migrates, the nuclear membrane disintegrates dispersing its contents into the cytoplasm. During hydration all yolk globules fuse into plates and the oocyte expands greatly, stretching the granulosa and thecal cell layers. At this time, the granulosa cells in cross section appear as long, thin rectangles, the thecal cells are extremely flat and have a stringlike appearance, and the zona radiata is very thin and lacks striations. Hydrated oocytes are the most ephemeral of all oocyte classes since this stage lasts for less than a day, whereas the other stages are always present in reproductively active anchovy ovaries. Migratory nuclei may be seen as early as 24 h before ovulation, but hydrated oocytes in which all globulues are fused to form yolk plates do not occur earlier than 12 h before spawning. We have never observed atresia in hydrated oocytes; apparently, in northern anchovy, nearly all hydrated oocytes are ovulated.

Atretic Stages

The nomenclature and general characteristics used for the four atretic stages given below follow those of Bretschneider and Duyvene de Wit (1947) and Lambert (1970a). In the initial stage of the atretic process (alpha (α)), the entire oocyte is resorbed including the yolk, if present, by the hypertrophying granulosa cells of the follicle. In the next stage (beta (β)), the major degeneration and resorption of the follicle (granulosa and thecal cells) occurs. In the third (gamma (γ)) and fourth (delta (δ)) atretic stages, regression of the theca and granulosa cells continues, greatly reducing the size of the follicle, and a yellow-brown pigment appears. The histological characteristics used to identify these stages are outlined below.

1) Alpha (α) Stage Atresia—In the alpha stage of atresia the oocyte is resorbing leaving only the follicular layers. The early phase of alpha stage atresia is characterized by the disintegration of the nucleus, evident by an irregular shape, and a granular, dark basophilic staining, and the disintegration of some of the yolk globules, indicated by less refractive globules, fused globules, or globules expanded and of less regular shape (Fig. 2a, b, c). The zona radiata slowly dissolves as indicated by the loss of striations and uneven diameter (Fig. 2b). In subsequent phases of alpha atresia, granulosa cells enlarge and, upon rupture of the zona radiata, invade the degenerating oocyte (Fig. 2d). Yolk adjacent to the invading granulosa cells liquifies (loses all structural integrity and appears as a homogeneous eosinophilic area) and becomes phagocytized by the granulosa cells as indicated by the presence of yolk in the vacuoles of these cells. The basophilic staining cytoplasm is also resorbed by the granulosa cells. In the alpha stage of atresia, blood capillaries and vessels are numerous in the thecal connective layer which does not proliferate or invade the oocyte but remains as a thin layer covering the granulosa cells. The alpha stage ends when resorption of the oocyte is complete (all cytoplasm and yolk are gone). The resulting structure (beta stage) is usually much smaller than the original oocyte. The subsequent atretic stages (beta-delta) are steps in the resorption of the remaining follicle and the structure at this point is called an atretic follicle, the term atretic oocyte being reserved for only the alpha stage of atresia.

In unyolked oocytes the alpha stage process is similar but without yolk (Fig. 2e, f). The nucleus

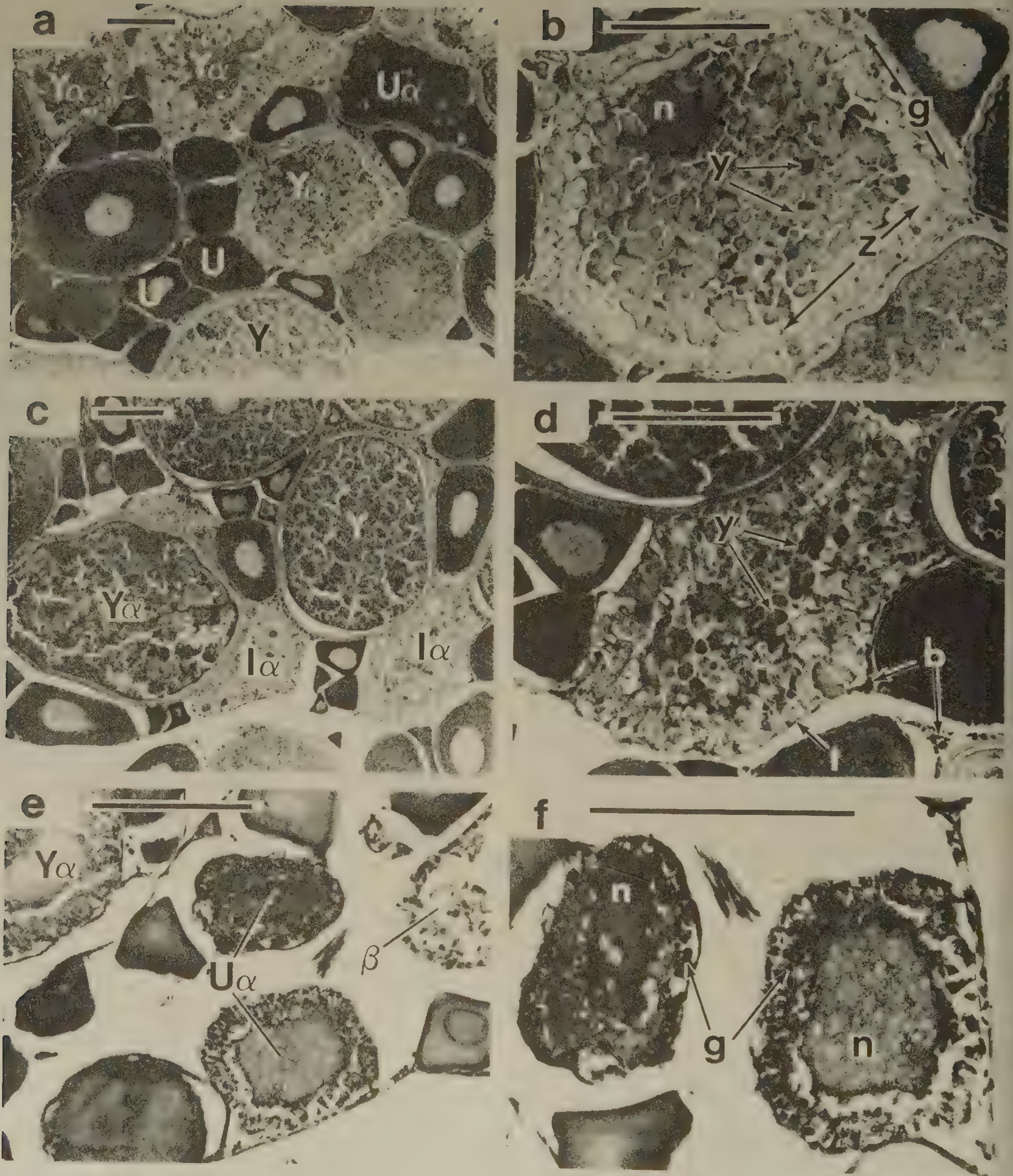

FIGURE 2.—Alpha (α) stage atresia in yolked (Y) and unyolked (U) oocytes (bar = 0.1 mm). a) and b) Yolked oocyte undergoing alpha atresia (Yα). Notice dark irregular nucleus (n), uneven dissolving zona radiata (z), and hypertrophic granulosa cells (g); (Uα = alpha atresia of a large unyolked oocyte). c) and d) Only remnants of yolk (y) remain among the invasive phagocytizing granulosa cells in this late phase of alpha atresia (Iα). Note also the thecal layer (t) and the closely associated red blood cells (b). e) and f) Unyolked oocytes in the alpha stage of atresia (Uα), note enlargement of granulosa (g) and disintegration of nucleus (n). (Yα = alpha yolked atretic oocyte, β = beta atresia.)

disintegrates, the thin prezona radiata (if present) dissolves and the granulosa cells enlarge, and, with only a slight proliferation, phagocytize the unyolked oocyte. When resorption is complete, all that remains is the follicle.

2) Beta (β) Stage Atresia—Initially the beta stage atretic follicle is a compact structure composed of numerous disorganized granulosa cells surrounded by a thin thecal and blood vessel layer. The nucleus of some of the granulosa cells is pycnotic and many of the cells contain a large intracellular vacuole that may be empty or contain amorphous particles. Occasionally one or more large intercellular cavities may exist among the granulosa cells (Fig. 3b, d). Preovulatory beta stage atretic follicles containing such cavities may easily be confused with postovulatory follicles (older than 48 h) and, as a consequence, we do not age postovulatory follicles older than 48 h (Hunter and Goldberg 1980). In addition, small (older) beta stage atretic follicles from yolked oocytes (Fig. 3c, d) are indistinguishable from beta stage atretic follicles from unyolked oocytes. Thus, we do not identify the original oocyte type undergoing atresia in beta or subsequent atretic stages; such distinctions are made only for alpha stage atretic oocytes.

Three different patterns of atresia may occur at the conclusion of the beta stage: 1) The follicle may follow the classic pattern outlined by Bretschneider and Duyvene de Wit (1947) and pass through subsequent gamma and delta stages (both characterized by increased pigmentation, see below); 2) the follicle may be completely resorbed during the beta stage leaving no histological characteristics that can be identified; and 3) the follicle may pass directly from a beta stage structure to a delta stage structure without passing through the intervening gamma stage. In northern anchovy, either the duration of the gamma stage is very short or few follicles pass through the gamma stage into the delta stage, because in regressing ovaries the incidence of gamma stages is very low compared with those of either beta or delta stages.

3) Gamma (γ) Stage Atresia—The gamma stage atretic follicle is usually much smaller than the typical beta stage follicle (Fig. 3e). The granulosa cells contain flocculent material of light-yellow hue and have nuclei of very irregular shape. The granulosa cells are surrounded by many fewer thecal cells and blood vessels than occur in the beta stage atretic follicles. Occasionally we see an atretic follicle of quite different appearance in anchovy ovaries which we classify as a gamma stage atretic follicle; they are included in the gamma stage because they also contain flocculent material of light-yellow hue. In this case, the flocculent yellow material is extracellular rather than intracellular, and the material is encapsulated by a layer of granulosa and thecal cells. It is possible that the extracellular flocculent material is produced by the disintegration of granulosa cells.

4) Delta (δ) Stage Atresia—The diagnostic characteristic of this stage is the presence of a dark yellow-brown, finely granular pigment in the granulosa cells (Fig. 3f). The delta stage atretic follicles are normally very small structures typically composed usually of 2-20 granulosa cells in the ovarian connective tissue stroma. Thecal cells and blood vessels no longer encompass the granulosa cells.

In our laboratory work 3-4 levels of abundance were recorded for each of three atretic classes seen in anchovy ovaries (alpha, beta, and gamma+delta stages). The gamma and delta stages were combined since gamma stages were rare. In addition, the alpha stage atretic class was further subdivided into three groups depending on the type of oocyte undergoing atresia (unyolked, partially yolked, and yolked oocytes). In the discussion that follows we have combined some of the abundance levels and have considered only what we believe to be the most diagnostic atretic characteristics, although all atretic characteristics as originally tabulated are given in Tables 1 and 2. The system of atretic classifications was further simplified in our presentation of the analysis of sea-caught specimens, but that will be discussed subsequently.

RESULTS

Rates of Atresia in the Laboratory

The speed at which yolked oocytes were resorbed was striking. In the first sample (elapsed time from onset of starvation = 3 d) the ovaries of 11 of the 24 females (46%) had yolked oocytes in the alpha stage of atresia (Table 1). By the 13th day, half of the females no longer had yolked oocytes, and in the rest of the females 50% or more of their yolked oocytes were in the alpha stage of oocyte

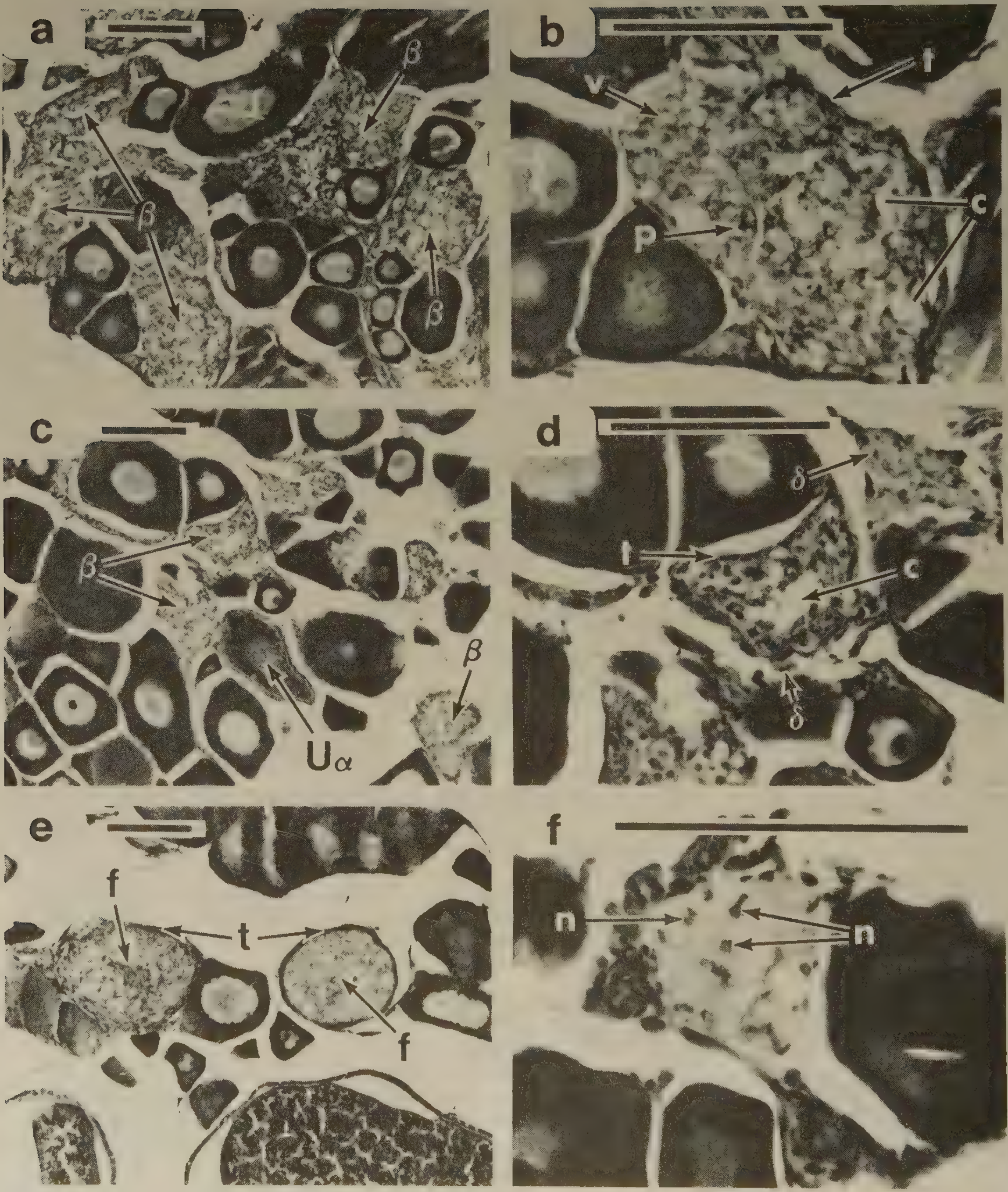

FIGURE 3.—Stages of atresia following after complete yolk absorption (bar = 0.1 mm). a) and b) Typical beta (β) stage atresia. Note the disorganized granulosa cells with some pycnotic nuclei (p) or intracellular vacuoles (v) (t = outer layer of thecal cells, c = intercellular cavities). c) and d) Disintegration of granulosa continues in these older beta (β) stage atresia. Note the large intercellular cavity (c) and the prominent, contracted thecal cell layer (t). Also present is an unyolked oocyte in early alpha (Uα) stage and several delta (δ) stage atresia cells. e) Two types of gamma (γ) atresia seen in northern anchovy ovaries. Note flocculent material (f) and the thecal layer (t). f) Delta (δ) stage atresia characterized by dark yellow fine granular pigment and an irregular nucleus (n).

TABLE 1.—Percentage of northern anchovy females with ovaries containing various levels of alpha stage atresia during starvation and after the resumption of feeding.[1]

Elapsed time from capture (d)	Feeding condition			Percentage of ovaries with levels of alpha stage atresia									
				Unyolked oocytes[2]			Partially yolked oocytes[2]			Yolked oocytes[3]			
	Starved	Fed	N	None	$N \leq 5$	$N > 5$	None	$N \leq 5$	$N > 5$	None	$F \leq 50\%$	$F = 50\text{-}90\%$	$F \geq 91\%$
3	X		24	79	13	8	46	29	25	50	33	0	13
6	X		21	19	14	67	14	14	62	5	10	19	48
9	X		24	12	17	71	0	58	34	0	8	17	42
13	X		20	10	15	75	20	15	20	0	0	5	40
16	X		24	0	12	88	4	17	17	0	0	0	8
20	X		22	0	36	64	0	0	4	0	0	0	4
23	X		23	9	39	52	0	4	13	0	0	0	0
27	X		23	4	57	39	0	0	0	0	0	0	0
34		X	23	70	17	13	4	0	0	0	0	0	0
41		X	18	83	17	0	17	0	0	17	0	0	0
62		X	22	90	5	5	64	9	9	36	23	0	0

[1] Feeding begins on the 28th day.
[2] N = mean number of atretic oocytes per 6 μm section.
[3] F = mean percentage of atretic oocytes per 6 μm section.

TABLE 2.—Percentage of northern anchovy females with ovaries containing various levels of beta and gamma+delta stage atresia and yolked oocytes during starvation and after the resumption of feeding.[1]

Elapsed time from capture (d)	Feeding condition			Percentage of ovaries with levels of atresia									Oocyte types	
				Beta stage atresia[2]			Beta stage atresia with no yolked oocytes[2]			Gamma+delta stage atresia[2]				
	Starved	Fed	N	None	$N \leq 5$	$N > 5$	None	$N \leq 5$	$N > 5$	None	$N \leq 5$	$N > 5$	Yolked oocytes present	Only partial and unyolked oocytes present
3	X		24	71	21	8	0	4	0	92	4	4	96	4
6	X		21	24	24	52	0	5	14	71	24	5	81	19
9	X		24	4	8	88	0	0	33	88	8	4	67	33
13	X		20	0	15	85	0	10	45	60	25	15	45	55
16	X		24	0	12	88	0	12	79	16	46	38	8	92
20	X		22	0	9	91	0	9	86	9	36	55	4	96
23	X		23	0	17	83	0	17	83	13	26	61	0	100
27	X		23	0	44	56	0	44	56	26	35	39	0	100
34		X	23	35	48	17	35	48	17	4	13	83	0	100
41		X	18	88	6	6	78	0	6	0	28	72	17	83
62		X	22	82	18	0	35	5	0	0	50	50	59	41

[1] Feeding begins on the 28th day.
[2] N = mean number of atretic follicles per 6 μm section.

resorption (Fig. 4). None of the females sampled on the 23d day had yolked oocytes, indicating that all yolked oocytes had passed through the alpha stage of atresia by this time.

The resorption of unyolked and partially yolked oocytes began just as rapidly as did the resorption of yolked oocytes. The percentage of females with atretic unyolked oocytes in the alpha stage increased sharply from 21% on the 3d day of starvation to 90% on the 13th day. Throughout the rest of the 27-d starvation period nearly all of the females (90-100%) had some unyolked oocytes in the alpha stage of atresia, indicating a continual recruitment of atretic follicles from the unyolked and partially yolked oocyte classes. Thus, alpha stage unyolked and partially yolked oocytes are present in regressing ovaries for a much longer period than is the alpha stage of yolked oocytes. This difference probably is due to the greater number of unyolked and partially yolked oocytes in mature ovaries. Yolked oocytes constitute <1% of the total number of oocytes present in mature ovaries.

The incidence of beta stage atretic follicles also increased sharply over the first 9 d of the starvation period and followed a pattern similar to that described for the incidence of alpha atresia from unyolked eggs (Fig. 4). After attaining a high value on the ninth day the incidence of beta atresia remained high until the end of the starvation period as atretic follicles from yolked and unyolked oocytes degraded from the alpha to the beta stage of atresia. Incidence of gamma+delta stages (the third and fourth stages of follicle degeneration) increased later than did alpha and beta stages and remained high after the onset of feeding.

Once feeding resumed (day 28), rapid resorption of yolked and unyolked follicles ceased and the

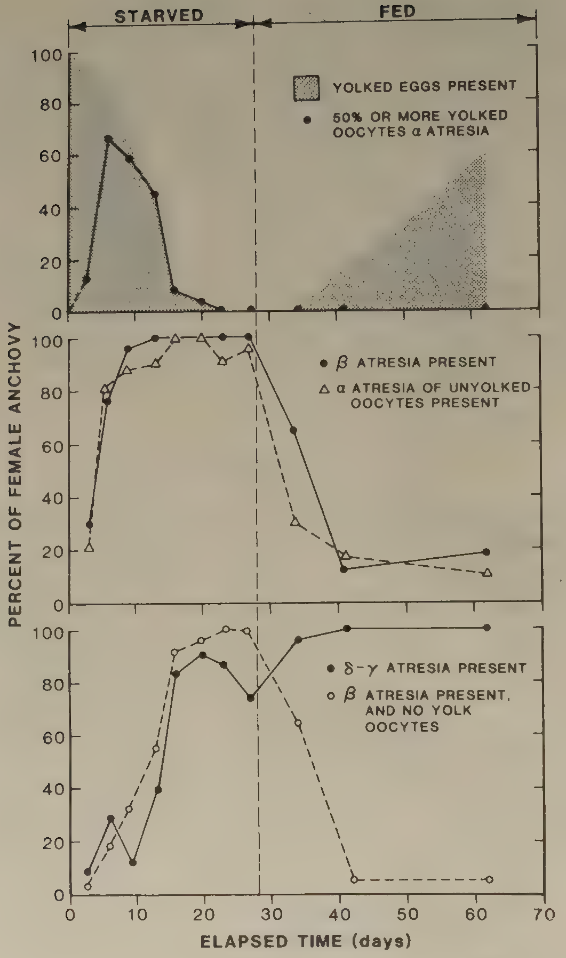

FIGURE 4.—Percentages of captive female northern anchovy with ovaries having various atretic characteristics during a 27-d starvation period and after the onset of feeding. Each percentage is calculated from a sample of 18-24 females (see Tables 1 and 2); alpha, beta, and gamma through delta stages of atretic follicles are those defined by Bretschneider and Duyvene de Wit (1941).

dominant process became maturation rather than resorption. This was indicated by sharp declines in the percentages of females with alpha stage atresia of unyolked oocytes and beta stage atretic follicles, and the reappearance of yolked oocytes (day 41). After only 1 wk of feeding the percentage of females with alpha stage atresia from partially unyolked oocytes dropped from 96 to 30%.

Some inferences can be drawn from these data regarding the duration of atretic stages. The sharp and simultaneous decline in beta stage atretic follicles and alpha stage atresia of unyolked oocytes (following the onset of feeding) indicates that alpha and beta stages must have a short and similar duration. The duration of alpha and beta atresia probably is <2 wk, since the incidence of these two stages dropped to very low levels 2 wk after the onset of feeding; a lag of about 1 wk existed between the first high incidence of females with beta atresia (9 d) and that for gamma+delta (16 d), indicating that the duration of the beta stage may be about 1 wk. The continued high incidence of gamma+delta stages of atretic follicles long after the onset of feeding indicates that these late atretic stages must persist in the ovary for much longer periods than alpha or beta stages. Although gamma+delta stages were present in all ovaries on the last day of the experiment their abundance within an ovary had decreased indicating that even the delta stage would eventually disappear, eliminating the last histological sign of past reproductive activity. We conclude from these inferences that the alpha and beta stages persist in the ovary for 1 wk or less whereas gamma+delta stages persist for over a month, but eventually all signs of past reproductive activity are lost.

The occurrence of alpha stage atresia of yolked oocytes is the best characteristic to use to back-calculate the time of past reproductive activity in field-caught specimens because the stage is of relatively short duration and the time required to resorb all yolked oocytes is relatively short. On the other hand, alpha stage atresia of unyolked oocytes, and beta and gamma+delta stages are less useful for back-calculations because these stages may occur in an ovary for extended periods while atretic oocytes are recruited from the large reservoir of unyolked oocytes in the ovary. In addition, estimates of the time since the onset of atresia in ovaries without yolked oocytes (using the incidence of beta or gamma+delta atretic stages) will always be uncertain because atresia of unyolked oocytes may occur at low levels in immature or developing ovaries as well as in regressing ovaries.

For the laboratory specimens, we calculated the average elapsed time from the onset of ovary resorption using various classes of alpha stage atresia of yolked oocytes and beta atresia in ovaries without yolked oocytes (Table 3). We prefer the criteria of 50% or more of the yolked oocytes with alpha stage atresia because it is likely that no spawning will occur in such females. The average duration of this stage (alpha, yolked, ≥50%) in the starving laboratory females was about 9 d and ranged from <3 to 20 d from the onset of starvation.

Starvation may have induced a higher rate of

TABLE 3.—Mean and maximum duration of various atretic characteristics of the ovaries of starved northern anchovy.

Atretic characteristics	Mean duration (d)	Maximum duration (d)
Alpha atresia of yolked oocytes present	8.0	20
Alpha stage atresia in:		
<50% of yolked oocytes	4.5	9
50-90% of yolked oocytes	8.1	13
91% or more of yolked oocytes	9.3	20
50% or more of yolked oocytes	9.0	20
No yolked oocytes present and beta atresia present	>16	>27

oocyte resorption than usually occurs under natural conditions. Variation in the female nutritional state, food ration, water temperature, day length, and a host of other variables may affect rates of atresia. In addition, field data indicate (see next section) that some spawning may occur in females with low to moderate levels of alpha (yolked) atresia, indicating that such stages may persist under natural conditions for extended periods. Despite these uncertainties we believe that our laboratory estimates of atretic rates are useful for making a rough estimate of the minimum time elapsed since the end of the spawning season in sea-caught females.

Natural Rates of Atresia

In this section we analyze sea data taken since 1977 for the occurrence of four ovarian atretic states in a northern anchovy population:

Atretic state 0—no alpha atresia of yolked oocytes (yolked oocytes present).

Atretic state 1—alpha atresia of yolked oocytes where <50% of the yolked oocytes are affected.

Atretic state 2—alpha atresia of yolked oocytes where 50% or more of the yolked ooctyes are affected (Fig. 5a, b).

Atretic state 3—ovaries with no yolked oocytes present and beta stage atresia present (Fig. 5c).

In addition to the atretic condition of the ovary, we also include histological evidence of recent or imminent spawning using the system of Hunter

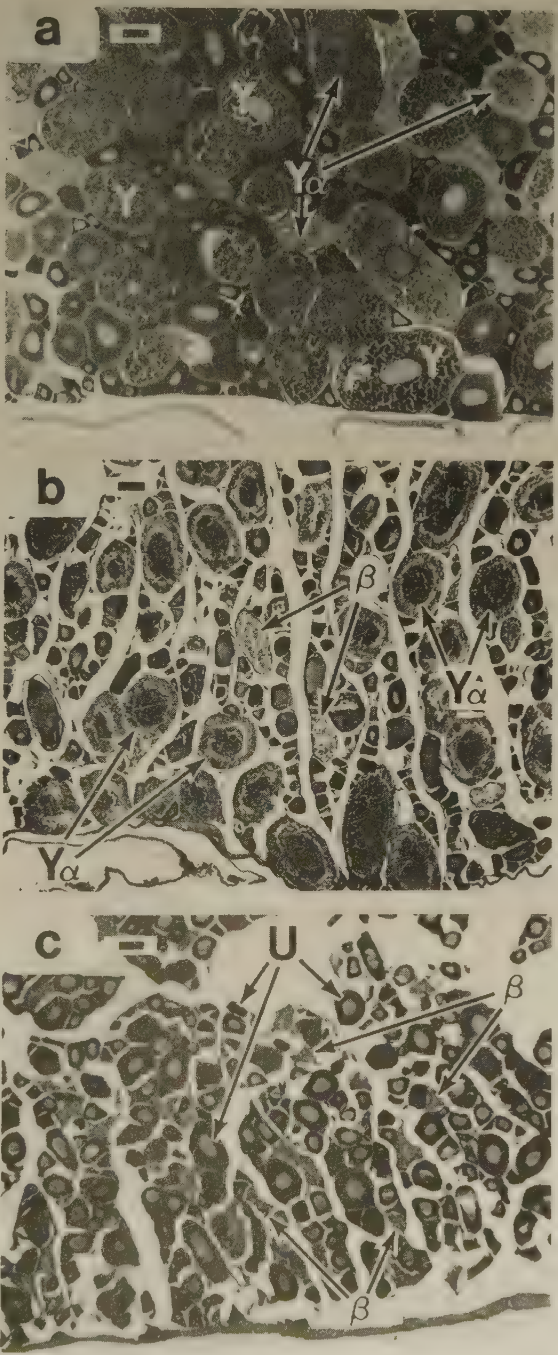

FIGURE 5.—Northern anchovy ovaries with increasing atresia states (bar = 0.1 mm). a) 50% of all yolked oocytes (Y) are in an alpha (α) stage of atresia (both early and late are counted). This is the division point between atretic state 1 and atretic state 2. b) 100% (all) yolked oocytes are in an alpha stage of atresia (Yα). Also present are a few unyolked alpha atretic oocytes and several beta (β) stage atretic follicles. This is still in atretic state 2. c) All yolk has been resorbed leaving only unyolked oocytes (U) and many beta (β) stage atretic follicles. This is atretic state 3.

and Goldberg (1980), i.e., presence of hydrated eggs (imminent spawning), day 0 or new postovulatory follicles (spawning on the night of capture), and 1-d-old postovulatory follicles (spawning on the night before capture). We also include the number of females judged to have inactive or immature ovaries with no evidence of atresia. All data on the incidence of reproductive states are given in Table 4. In the discussion that follows we select and regroup these data in various fashions to test hypotheses and document trends.

Incidence of Spawning in Atretic Females

An important assumption underlying interpretation of ovarian atresia is that the spawning season has or is going to cease, in other words, the probability of spawning in females with atretic ovaries would be expected to be low. To test this assumption we selected from Table 4 the females which had alpha stage atresia of yolked oocytes (atretic states 1 and 2) or yolked oocytes without alpha atresia (atresia state 0) and calculated the percentage of these females that had hydrated oocytes, new (day 0) postovulatory follicles, and 1-d-old postovulatory follicles. Of the females classed in atretic state 1 (females with <50% of the yolked oocytes in alpha stage of atresia), 14% showed evidence of recent or imminent spawning (postovulatory follicles or hydrated oocytes); 29% of the females without atresia showed evidence of spawning (Table 5). Only 1% of those in atretic state 2 (females 50% or more atretic yolked oocytes) had recently been reproductively active. That 1.8% of females in atretic state 1 had hydrated eggs and 3.7% had age 0 d postovulatory

TABLE 4.—Numbers of female northern anchovy in various atretic and reproductive states northern California

Collection dates number of mature females/collection	Atretic state[1]	Hydrated oocytes	Postovulatory follicles 0 day[2]	Postovulatory follicles 1 day[3]	Yolked oocytes	No yolked oocytes	Immature no histology[4]	Total
1977	0	1	2		13	4		20
09/09-09/10	1							0
	2							0
(10)	3					3		3
	x	1	2	0	13	7	0	23
1978	0				1			1
05/07-05/11	1			1	5			6
	2				4			4
(10)	3					6		6
	x	0	0	1	10	6	0	17
1979	0	39	44	52	279	89	110	613
01/26-02/16	1			1				1
	2				1			1
(10)	3					2		2
	x	39	44	53	280	91	110	617
1979	0	16	51	45	284	27	18	441
03/22-04/14	1		1	5	36			42
	2				6			6
(10)	3					16		16
	x	16	52	50	326	43	18	505
1979	0			1	8	4		13
06/09-06/19	1				3			3
	2				1			1
(12)	3					16		16
	x	0	0	1	12	20	0	33
1979	0				9	31		40
09/19-09/23	1							0
	2				5			5
(10)	3					25		25
	x	0	0	0	14	56	0	70
1980	0	25	72	52	241			390
03/20-04/10	1				9			9
	2				1			1
(20)	3					2		2
	x	25	72	52	251	2	0	402
1980	0		4	9	63	8	6	90
04/24-04/27	1				11			11
	2				14			14
(20)	3					63		63
	x	0	4	9	88	71	6	178

[1] Atretic state 0 = no alpha stage atresia of yolked oocytes.
state 1 = alpha stage atresia of yolked oocytes present but <50% oocytes affected.
state 2 = alpha stage atresia of yolked oocytes present, 50% or more oocytes affected.
state 3 = no yolked oocytes present and beta stage atresia present.

follicles indicate that some of the females in atretic state 1 spawn despite the atretic condition of their ovaries. On the other hand, only two females classed in atretic state 2 had a recent history of spawning. These two females had few yolked oocytes remaining, all but one was in alpha atresia. This atresia may have increased or even started during the time elapsed between hydration and capture. In short, the females in atretic state 2 probably did not spawn in the highly atretic state in which they were captured. No doubt exists that females with moderate levels of ovarian atresia are capable of spawning because they often are hormonally induced to do so in the laboratory. In summary these data indicate that significant numbers of females in atretic state 1 may continue to spawn under natural conditions, although the probability of spawning appears to be about half that of fish without ovarian atresia. Few or none of the females in atretic state 2 continue to spawn indicating that this stage is probably the best one to use to calculate cessation of spawning in the population.

Forcasting the end of Spawning Using Ovarian Atretic States

In our laboratory study atretic state 1 had an average duration of about 5 d and atretic state 2, 9 d; state 3 was in excess of 16 d and probably persists for 30 or more days (Table 3). In the sea, linear projections of the end of the spawning season from early incidence of atresia is not realistic since the numbers of females with regressing ovaries would be expected to increase sharply at the end of the season.

listed in order of collection dates for southern and Baja California (1977-82) and for (1979, 1982).

Collection dates number of mature females/collection	Atretic state[1]	Hydrated oocytes	Postovulatory follicles		Yolked oocytes	No yolked oocytes	Immature no histology[4]	Total
			0 day[2]	1 day[3]				
1980	0			3	32	11		46
05/15-05/28	1		1		5			6
	2				2			2
(20)	3					16		16
	x	0	1	3	39	27	0	70
1981	0	119	122	148	862	58		1,309
02/05-03/06	1		2	1	19			22
	2				3			3
(15)	3					10		10
	x	119	124	149	884	68	0	1,344
1981	0	77	96	113	559	7		852
04/01-04/19	1		3	2	57			62
	2		1		45			46
(15)	3					19		19
	x	77	100	115	661	26	0	979
1981	0		2	1	7			10
04/15-04/30	1				5			5
	2				8			8
(15)	3					7		7
	x	0	2	1	20	7	0	30
1982	0	104	101	189	1,172	52	8	1,626
01/28-03/08	1	2	2	10	32			46
	2				2			2
(15)	3					6		6
	x	106	103	199	1,206	58	8	1,680
1979[5]	0		1		42			43
03/20-03/22	1		1		40			41
	2				41			41
(30)	3					25		25
	x	0	2	0	123	25	0	150
1982[5]	0	2			27	2	11	42
01/22-01/25	1	3		2	14			19
	2			1	5			6
(15)	3					13		13
	x	5	0	3	45	16	11	80

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[2] New postovulatory follicles <24 h old.
[3] Postovulatory follicles about 24 h old.
[4] Female not examined histologically, ovary ≤1% of body weight.
[5] Female northern anchovy from northern California; rest of females were from southern and Baja California.

TABLE 5.—Percentage of northern anchovy females taken from 1977 to 1982[1] that were classed in three atretic states that occurred in each of five reproductive classes.

		Reproductive state					
			Postovulatory follicles				
Atretic state	Percent yolked oocytes with alpha stage atresia	Hydrated oocytes (%)	0 day (%)	1 day (%)	Spawning recent or imminent[2] (%)	No evidence of recent spawning[3] (%)	Total number of females
0	0	7.5	9.7	12.0	29.3	70.7	5,090
1	<50	1.8	3.7	8.1	13.6	86.4	273
2	≥50	0	0.7	0.7	1.4	98.6	140

[1] Calculated from data given in Table 4; only females with yolked oocytes are considered.

[2] Females with either hydrated oocytes or postovulatory follicles ages 0 or 1 d (the sum of the first three columns).

[3] Females with yolked oocytes but without hydrated oocytes or postovulatory follicles.

This nonlinearity becomes obvious when the end of the spawning season is extrapolated from numbers of females classed in atretic state 2. For example, of the 1,620 mature females taken during the peak of spawning (28 January-18 March 1982) in southern California (Table 4), only two were in atretic state 2 and 1,612 had yet to pass through state 2. Since laboratory data indicate that about 9 d are required to pass through atretic state 2, it would require (1,612/2) × 9, or over 7,000 d for the entire population to become atretic at the rates of atresia observed in February, which, of course, is nonsense. Projections of the end of the spawning season using higher rates of atresia taken in April in southern California (24-27 April 1980) give a more realistic projection ((87/14) × 9 = 56 d). Such an arithmetic projection may be inappropriate for collections which have a very high rate of atresia such as those taken in Monterey in March 1979 ((84/41) × 9 = 18 d), and a geometric model might be preferable. The point we wish to emphasize is that atretic rates are nonlinear over the season with the rate increasing markedly as the season closes. Thus only samples taken near the close of the spawning season are of value for forecasting the end of spawning for the population.

Seasonal Changes in Atresia Among Females of Different Lengths

To evaluate how atretic rates change among females of different lengths, we segregated our data into two length classes (females $\leq$10 cm SL and those $>$10 cm SL) and calculated the percentage of mature females that had atretic ovaries (atretic states 1-3 combined). Mature is defined here as all females except those which have yet to reach first maturity (small females with small immature non-atretic ovaries). We also calculated the fraction of females in each length class with 1-d-old postovulatory follicles, a measure of the percentage of females spawning daily (Hunter and Goldberg 1980).

In every case, regardless of cruise or season, small females ($\leq$10 cm SL) consistently had a higher rate of ovarian atresia than did larger ones ($>$10 cm SL) (Table 6). This is a strong trend as the probability of such an event (9 pairs of the same sign) is $(1/2)^9$. In addition, the difference between pairs was statistically significant (chi-square test) even when the levels of atresia were quite low. For example, in February-March 1981, only 4.1% of the small females and 1.9% of the large females were atretic, yet this difference was significant at $P < 0.05$ using the chi-square test. As would be expected, the percentage of females with atretic ovaries increased in both length classes as the season progressed from January through June.

The consistency of the differences in the incidence of atresia between large and small females indicates that the smaller ones must have a much shorter spawning season than larger ones. Females $<$10 cm long are typically about 1-yr-old and are in their first spawning season whereas those longer than 10 cm are predominantly 2-3 yr old and have spawned during the previous seasons. These data indicate that the first spawning season of females may be quite short with significant numbers of females leaving the spawning population in early April, while the older fish continue to spawn. That the rates of atresia in young fish were always higher even in the peak months of spawning such as February and March indicates that a small percentage of small females may only spawn a few times during the season in contrast to the older females which appear to be spawning at about weekly intervals for months. The fraction of small females spawning per day would be expected to be less than larger females since the small females have a higher incidence of ovarian atresia. We calculated the fraction of females spawning per

TABLE 6.—Percentage of mature northern anchovy females in two length classes with atretic ovaries. Females from north of Point Conception and groups with fewer than nine females per length class excluded.

Cruise period			Number of mature females[1]		Percent of mature females with atretic ovaries[2]		Fraction mature females spawning per day percent[3]	
From	to	year	≤10 cm	>10 cm	≤10 cm	>10 cm	≤10 cm	>10 cm
01/26	→02/16	1979	121	297	1.7	0.7	8.0	15.9
01/28	→03/18	1982	97	1,523	14.6	2.6	14.1	12.2
02/05	→03/06	1981	462	824	4.1	1.9	10.2	13.7
03/20	→04/10	1980	68	334	8.8	1.8	11.7	15.2
03/22	→04/14	1979	30	430	23.3	13.3	3.8	11.8
04/01	→04/19	1981	102	870	39.2	10.0	10.5	12.9
04/24	→04/27	1980	64	100	96.9	26.0	0	8.6
04/15	→04/30	1981	10	20	80.0	60.0	0	5.3
05/15	→05/28	1980	15	44	73.3	29.5	6.2	4.4

[1] All females given in Table 4 except those with immature ovaries and those not examined histologically.

[2] All females in atretic states, 1, 2, and 3 combined.

[3] Fraction of females spawning = F, where $F = \dfrac{m_{1i}}{2m_{1i} + m_{ni}}$

m_{ni} = mature nonspawning females, and m_{1i} = females with 1-d-old postovulatory follicles.

day for the two length classes to test this assumption. We used the Stauffer and Picquelle (footnote 3) method for estimating spawning fraction as it corrects for biases in the numbers of females with hydrated eggs, i.e.,

$$F = \frac{M_{1i}}{2M_{1i} + m_{ni}}$$

where F = fraction of females spawning per day, M_{1i} = number of females with 1-d-old postovulatory follicles, and m_{ni} = number of mature females with no recent spawning history (females with postovulatory follicles or hydrated eggs are excluded). Examination of Table 6 indicates that differences in spawning fraction between the two size classes of females were much less distinct than were the differences in ovarian atresia. Using only the 8 cruises in which the numbers of females in each of the two length classes exceeded 10, the mean difference in spawning fraction (fraction for large females − fraction for small females) for the set of 8 cruises was +3.76% with 95% C.I. ±3.50% indicating a small difference in spawning frequency between the two length classes that is just barely significant at the 5% level. We believe the reason that differences in atretic fraction between large and small females are much more consistent than those in spawning fraction is that spawning fraction has a greater variability and a much more limited dynamic range than does the atretic fraction. Spawning fraction varies from 0 to about 16% and may be affected by time of day and schooling behavior (Hunter and Goldberg 1980). Atretic fraction varies from 0 to nearly 100%, is not linked to reproductive behavior, and consequently, is probably not affected by time of day or schooling.

DISCUSSION

Evaluation of Atretic Classification

Our objective was to evaluate the use of ovarian atretic states to characterize the reproductive biology of northern anchovy populations. We included in our analysis of laboratory data many atretic characteristics not used to construct the three atretic states utilized in the analysis of sea data. These additional characters could be used to create additional states or to more precisely delimit the existing ones. Our selection of characteristics was based in part on ease of identification since for population work thousands of histological sections were examined. Other considerations include the fact that statistical analysis indicated that classifiers frequently confused beta stage atretic follicles in yolked ovaries with postovulatory follicles older than 24 h, and, as a consequence, beta atresia was not used as a diagnostic character in ovaries with yolked oocytes. Alpha stage atresia was the most useful atretic stage because the type of oocyte (yolked) undergoing atresia is still discernible. In addition, alpha stage atretic oocytes can be easily distinguished from postovulatory follicles whereas this is not the case for later atretic stages.

Three atretic states were defined and applied to sea data. The incidence of all three atretic states combined was a sensitive index of the reproductive state of the population over the spawning season.

In fact, the atretic condition of the ovary was a more sensitive index of seasonal changes in the reproductive rate among size classes of females than was the incidence of spawning based on the presence of postovulatory follicles.

Atretic state 1 (<50% of yolked oocytes in the alpha stage of atresia) was not useful for estimating atretic rates in an absolute sense since this state appeared to persist in natural populations for extended and probably variable periods. Some spawning occurred among females classed in atretic state 1, although the frequency of spawning was less than half of that of females without ovarian atresia. Batch fecundity might also be reduced in females classed in atretic state 1, a speculation worth further study. Atretic state 1 was a useful index of atretic rates during peak spawning months. At such times it was the most common atretic condition and detection of differences in atretic rates among length classes was largely a function of the number of females in this state.

Atretic state 2 (50% or more of yolked oocytes in alpha atresia) persisted for about 9 d in the laboratory, and judging by its low frequency in field collections this state may have a similarly short duration in natural populations. Females with ovaries in this state rarely or never spawn, as might be expected, since more than half of the yolked oocytes are not viable. In addition, a short duration of this state also might be expected on the grounds that it seems maladaptive to prolong such a threshold condition. For the above reasons atretic state 2 seems to be the best absolute measure of the rates of ovary resorption in the population and the only state that might provide an accurate forecast of the end decline of reproduction in a population. Unfortunately, accurate forecasts of the end of spawning for a population can be made only near the end of the spawning season.

Atretic state 3 (no yolked oocytes with beta atresia present) identifies females in late postspawning condition. Such females cannot be separated from immature females on the basis of gonad weight or using gross anatomical criteria. This state persisted for about 30 d in the laboratory, but it may last much longer under natural conditions while the numerous small oocytes are resorbed. The laboratory data indicate that the duration of this state could be increased if the definitions were changed to include gamma+delta stages of atresia which have a longer life in the ovary than the beta stage. The laboratory data also indicated that even gamma+delta stages of atresia would eventually disappear from the ovary so that no signs of previous spawning activity would exist in a regressed ovary. It is doubtful that the duration of atretic state 3 or any late postspawning state will ever be accurately estimated because it is dependent on too many environmental circumstances. Nevertheless, this state is very useful in separating females in postspawning condition from females with no previous reproductive history. This is an essential distinction for estimating spawning biomass (Stauffer and Picquelle footnote 3) and for determining the size or age at first reproduction (Hunter and Macewicz 1980).

Possibly the most important future application of atretic classification of ovaries is for process oriented sea work on the reproductive biology of multiple spawning fish such as the northern anchovy. Such work does not require a large sample as do estimates of reproductive characteristics for an entire population. The reproductive state of an individual female can be accurately defined by the atretic criteria we have discussed, and the spawning state criteria described by Hunter and Goldberg (1980). The reproductive characteristics of a female can be related to its physiological state (age, fat content, biochemical composition, and instantaneous growth rate from otoliths or RNA/DNA ratios) and functional relationships established between reproduction and the environment. In this way the factors controlling the duration of the spawning season, and the total fecundity during the season, can be identified under natural conditions.

Biological Implications

Several important biological conclusions can be drawn from this work. Only a few attempts have been made to estimate the time needed for a follicle to disappear by atresia in vertebrates and no information exists for fishes (Byskov 1978). Our focus was on atretic rates of all oocytes in the ovary and not on an individual follicle; nevertheless, the striking speed with which all yolked oocytes passed through the initial stages of atresia indicate that the rate for individual follicles must be high. Similar rates were observed in the guppy by Lambert (1970a). In the guppy, alpha stage atresia of yolked oocytes appears about 1 d after parturition, and beta stage atresia appeared about 2 d after the first alpha stages were detected; beta stages persisted for only 11 d. In the anchovy, the average time for all yolked oocytes in the ovary to pass through alpha atresia was 8.0 d and the maximum time was 29 d. Thus the effect of atresia on fecundity may be underestimated since the duration of atretic stages is short and a small standing stock of atretic oocytes could be an indication of a high loss rate. On the other hand, laboratory studies seem to indicate that atretic rates are not sufficiently high to account for the differences in fecundity observed when fish are fed high and low rations (Tyler and Dunn 1976; Wootton 1979). The duration of the atretic stages in these studies was unknown, however.

Additional evidence for the volatility of the reproductive state of anchovy is an important contribution of this study. Our laboratory data indicated that given a shortage of food the ovary can be rapidly resorbed leaving no trace of former reproductive activity in a few months or less, but when given sufficient food atresia stopped, maturation and vitellogenesis resumed, and a reproductively active ovary was rapidly reformed within 35 d. Clearly, in such multiple spawning fishes as the anchovy, more than one spawning season per year is possible given the appropriate environmental conditions. This may explain the occurrence of a second annual spawning period in the Peruvian anchoveta (Santander and Castillo 1976) and the occasional heavy fall spawning of the northern anchovy (Smith 1972). That active ovaries are consistently produced from small, inactive ones in 30-60 d in the laboratory (Leong 1971; Hunter and Leong 1981) and that some reproductively active females are found the year around also supports this view.

Food shortage does not always lead to regression of the ovary in anchovy or any other multiple spawning fishes. In addition to food ration, regression of the ovary also depends upon the level of energy reserves, the timing of the reproductive cycle, and perhaps certain environmental conditions such as temperature and day length. For example, starvation of 40-80 d did not block the initial increase in the size of ovaries of the goby *Gillichthys* at the start of the reproductive cycle in July but only 23 d of starvation resulted in ovarian regression in January when active vitellogenesis was occurring (de Vlaming 1971). Similarly we noted in a preliminary experiment that starving anchovy of 25% greater wet weight than those used in this study produced a slower regression of the ovary over a 36-d period than occurred in the present study. The present study is more representative of natural conditions since the fish were taken in midspawning season when their ovaries were active whereas in the preliminary study the fish were taken out of season and fed heavily for 30 d to induce gonad maturation before the onset of the 36-d starvation period.

Another important conclusion from this study was that young female anchovy spawning for the first time probably have a much shorter reproductive season than do older females. Hunter and Leong (1981) estimated that the average female spawns about 20 times per year. Thus the older females must spawn considerably more often than 20 times per year, and probably contribute a much larger fraction of the reproductive output of the population than a proportionate share by weight. This indicates the importance of maintaining older fish in the population and that danger may exist if older fish are overharvested.

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LITERATURE CITED

BARR, W. A.
1963. The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* (L.) I. Cyclical changes in the normal ovary. Gen. Comp. Endrocrinol. 3:197-204.

BOUAIN, A., AND Y. SIAU.
1983. Observations of the female reproductive cycle and fecundity of three species of groupers (*Epinephelus*) from the southeast Tunisian Seashores. Mar. Biol. (Berl.) 73:211-220.

BOWERS, A. B., AND F. G. T. HOLLIDAY.
1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). Dep. Agric. Fish. Scotl., Mar. Res. 5:1-16.

BRETSCHNEIDER, L. H., AND J. J. DUYVENE DE WIT.
1947. Sexual endocrinology of non-mammalian vertebrates. Monogr. Prog. Res., Vol. II, Elsevier, N.Y.

BYSKOV, A. G.
1978. Follicular atresia. *In* R. E. Jones (editor), The vertebrate ovary: Comparative biology and evolution, p. 533-562. Plenum Press, N.Y.

CROSSLAND, J.
1977. Seasonal reproductive cycle of snapper *Chrysophrys auratus* (Forster) in the Hauraki Gulf. N.Z. J. Mar. Freshwater Res. 11:37-60.

DE VLAMING, V. L.
1971. The effects of food deprivation and salinity changes on reproductive function in the estuarine gobiid fish, *Gillichthys mirabilis*. Biol. Bull. (Woods Hole) 141:458-471.

1972. Reproductive cycling in the estuarine gobiifish *Gillichthys mirabilis*. Copeia 1972:278-291.

DE VLAMING, V., G. GROSSMAN, AND F. CHAPMAN.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31-39.

FULTON, W.
1898. On the growth and maturation of the ovarian eggs of Teleostean fishes. Annu. Rep. Fish. Board Scotl. 16: 88-124.

HOAR, W. S.
1965. Comparative physiology: hormones and reproduction in fishes. Annu. Rev. Physiol. 27:51-70.

HTUN-HAN, M.
1978. The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: seasonal changes in the ovary. J. Fish Biol. 13:351-359.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77: 641-652.

HUNTER, J. R., AND R. LEONG.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

HUNTER, J. R., AND B. J. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.

LAMBERT, J. G. D.
1970a. The ovary of the guppy, *Poecilia reticulata*. The atretic follicle, a *Corpus atreticum* or a *Corpus luteum praeovulationis*. Z. Zellforsch 107:54-67.
1970b. The ovary of the guppy *Poecilia reticulata*. The granulosa cells as sites of steroid biosynthesis. Gen. Comp. Endocrinol. 15:464-476.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

ROBB, A. P.
1982. Histological observations on the reproductive biology of the haddock, *Melanogrammus aeglefinus* (L.). J. Fish Biol. 20:397-408.

SAIDAPUR, S. K.
1978. Follicular atresia in the ovaries of non-mammalian vertebrates. Int. Rev. Cytol. 54:225-244.

SANTANDER, H., AND O. S. DE CASTILLO.
1979. El ictioplancton de la costa Peruana. Inst. Mar Peru Bol. 4:69-112.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

TYLER, A. V., AND R. S. DUNN.
1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. J. Fish. Res. Board Can. 33:63-75.

VROOMAN, A. M., P. A. PALOMA, AND J. R. ZWEIFEL.
1981. Electrophretic, morphometric, and merisitic studies of subpopulations of northern anchovy, *Engraulis mordax*. Calif. Fish Game 67:39-51.

WALLACE, R. A., AND K. SELMAN.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325-343.

WOOTTON, R. J.
1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. Lond. 44:133-159.

YAMAMOTO, K.
1956. Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. Fac. Sci. Hokkaido Univ., Ser. 6, Zool. 12:362-373.

ZANUY, S.
1977. Inducción a la puesta y estudio de la ovogénesis en un teleósteo marino: *Paracentropristis cabrilla* L. Invest. Pesq. 41:337-384.

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VISUAL THRESHOLD FOR SCHOOLING IN NORTHERN ANCHOVY *ENGRAULIS MORDAX*

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ABSTRACT

The visual threshold for schooling was determined for two groups of 50 adult northern anchovy in the laboratory. The index of dispersion and the mean distance to the nearest neighbor were used to measure changes in schooling as a function of light intensity. The threshold light intensity for schooling, 6×10^{-11} W cm^{-2} (2.6×10^{-4} mc), was estimated to occur at a depth of 30 m on a starlit night and at 38 m during a full moon, when the chlorophyll concentration is 0.2 mg Chl a m^{-3}. At 2.0 mg Chl a m^{-3} the threshold occurs at a depth of 8 m on a starlit night and at 20 m under full moon light. Sufficient light appears to exist at night within the upper 10 m for schooling to occur in most of the habitat of the anchovy. The vertical distribution of newly spawned anchovy eggs indicated that the maximum depth of spawning may be similar to the maximum depth of schooling and that the visual threshold for schooling could be used to forecast maximum spawning depth in the sea.

Vision plays a primary role in the maintenance of most fish schools in the sea. Other sense organs, particularly the lateral line, are important in coordinating movements and spacing of fish within the school (Pitcher et al. 1976), but it is unlikely that lateral line sense alone is sufficient for maintaining the integrity of schools at night in the sea. In fact, a large number of laboratory studies indicate that if light is sufficiently reduced, fish no longer maintain schools (Whitney 1969; Blaxter 1970). Thus the visual threshold for schooling and the depth of penetration of light probably determine the maximum depth at which pelagic fishes are able to school at night in the sea.

Our objective was to determine the visual threshold for schooling in adult northern anchovy, *Engraulis mordax*, and to use this information to forecast the maximum schooling depth for anchovy at night in the sea. This calculation is of ecological interest because the maximum depth for schooling is probably also the maximum depth for spawning and for nocturnal feeding. Anchovy spawn only at night and visual recognition of other fish is probably as essential for spawning as it is for schooling. During what we believe was spawning behavior, several males rapidly pursued a female over an irregular path, a tactic probably not possible using senses other than vision. This is a casual laboratory observation and requires further documentation, however. Northern anchovy feed at night as well as in the day (Loukashkin 1970; Hunter and Kimbrell 1980). Light may not be necessary for filter feeding, but it is essential for particulate feeding, although somewhat higher light levels may be required for feeding than for schooling (Hunter 1968). Anchovy migrate toward the surface at sunset (Mais 1974), and schools are less frequently detected at night using sonar and not detected with echo sounders (Smith 1970). Nevertheless, no doubt exists that schooling continues at night because the anchovy fishery is typically a night fishery and because profiles of schools are detectable at night owing to the bioluminescent disturbances their movements produce (Squire 1978).

METHODS

Apparatus and Laboratory Procedures

Two groups of 50 northern anchovy (group 1, mean length = 10.5 cm SL; group 2, = 9.8 cm SL) were maintained in a 4.6 m diameter tank supplied with running seawater (group 1, mean temperature = 16.9°C; group 2, 21.0°C). To simplify photographic analysis the school of 50 fish was constrained to a somewhat two dimensional form by maintaining them in water 45 cm deep. The fish were fed adult *Artemia* at the daily time of 1000, and the tank was cleaned 1 h after feeding.

The tank, which was constructed of blue vinyl, was located in a light tight rectangular enclosure in which the walls and ceiling were covered with white vinyl

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to diffuse the light. Four light sources were equally spaced around the periphery of the tank; the top of each being just below the tank rim. Each source consisted of a 30 W tungsten microscope lamp with reflector enclosed in a tube. On top of the tube were two color filters; a green acrylic plastic filter (#2414, Rohm and Haas), and a sealed petri dish containing a 5% $CuSO_4$ solution (by weight). To diffuse the light a translucent white acrylic filter (#W-2447, Rohm and Haas) was placed on top of the color filters and light transmitted by the white filter entered a white opal glass globe (13 cm diameter) that formed the top of the source. The lamps were operated for 5 h (10% of lamp life) before they were used to produce test levels of irradiance. These sources were used to produce four test levels of irradiance during a 12-h night. Additionally, four tungsten 100 W household lamps (unfiltered) with reflectors were used for the daytime level of irradiance. These lamps were placed at regular intervals around the perimeter of the tank near the ceiling. Light from these lamps reflected off the ceiling providing a uniformly diffuse illumination. The spectrum produced by the four sources (Table 1) resembles the greenish spectrum typical of anchovy habitat, but the spectrum used in the day was not different from a standard curve for a tungsten lamp and consequently contained an unnaturally high proportion of longer wavelength energy. Our term for the condition when all lamps were off was darkness; under these conditions light was not detectable by a dark adapted human observer and the irradiance was below the sensitivity of a 931A photomultiplier which can detect about 5×10^{-6} mc (meter candle).

To record the effect of light on the schools the fish were photographed from above the tank using a 35 mm automatic camera and flash attachment. The camera was controlled by a timer, and photographs were taken at 30-min intervals for 5 h during the 12-h day, at night in darkness, and at night at the test levels produced by the four sources. Night photographs were taken during a 5-h period commencing 2 h after the end of the 12-h day. Ten photographs were usually analyzed at each light level for each group, but in several tests, 1 or 2 photographs were not analyzed because not all 50 fish could be seen.

Two indices of schooling were calculated for each photograph: an index of dispersion (Pielou 1969), and the mean distance to the nearest neighbor (Hunter 1966). The dispersion index was calculated by superimposing a grid containing 326 quadrats over the projected image of the tank and counting the number of fish occurring in each quadrat. The variance mean ratio ($s^2/\bar{x}$) for the number of fish per quadrat was the index of dispersion. The index was calculated for each photograph, and an average index was computed for each light treatment (n = 8-10 photographs). A dispersion index of 1 indicates a random distribution, whereas higher values indicate aggregation (Pielou 1969) and imply the existence of schooling. Values < 1 imply a uniform distribution over the grid. The mean distance to the nearest neighbor was computed for a random subsample of 10 fish in a photograph. All 50 fish in a photograph were numbered and the subsample of 10 was selected by drawing the fish numbers from a table of random numbers. For each of the 10 fish in the subsample the distance in centimeters to its nearest neighbor was measured (distance between heads), a mean distance calculated for each photograph, and means

TABLE 1.—Spectral functions used to estimate the depth of occurrence of the visual threshold for schooling under the various water types and incident irradiances including spectral irradiance in the laboratory apparatus, moonlight at 3 m below water surface, starlight at the earth's surface (Munz and McFarland 1977), and the relative sensitivity of the dark adapted anchovy eye (*Engraulis encrasicholus*, Protasov 1964).

Wavelengths (nm)		Energy per 25 nm interval ($W\ cm^{-12}$)			Relative sensitivity anchovy eye
Mean	Interval luminaires	Laboratory luminaires	Moonlight at 3 m depth	Starlight at surface	
400	400-412	3.411×10^{-12}			
425	413-437	1.346×10^{-11}	6.109×10^{-10}	1.978×10^{-11}	0.16
450	438-462	3.402×10^{-11}	6.689×10^{-10}	2.418×10^{-11}	0.53
475	463-487	6.822×10^{-11}	6.820×10^{-10}	2.291×10^{-11}	0.85
500	488-512	9.631×10^{-11}	7.072×10^{-10}	2.374×10^{-11}	1.00
525	513-537	1.069×10^{-10}	7.067×10^{-10}	2.449×10^{-11}	0.75
550	538-562	9.618×10^{-11}	7.283×10^{-10}	5.125×10^{-11}	0.42
575	563-587	5.297×10^{-11}	6.881×10^{-10}	2.838×10^{-11}	0.22
600	588-612	[1]9.494×10^{-12}	5.481×10^{-10}	3.874×10^{-11}	0.08

[1] Wavelength interval = 588-600 nm.

for each light treatment. These measurements are indices of only one characteristic of a fish school, the tendency of individuals to maintain contact with each other and thereby remain in a social group. The polarization of individuals in a school is frequently included in definitions of schooling as the cohesive movements of a school require that fish maintain relatively constant headings and individual distances which gives the polarized appearance of moving schools. This characteristic of fish schools was not measured in our study, thus the visual threshold we estimated was one for the maintenance of schooling in the broadest sense, that is the existence of a group maintained by visual attraction.

Radiometric Procedures, Calibrations, and Computations

Radiometric equipment used in this study consisted of an Optronics spectroradiometer (model 714-V) (calibrated against a radiometric standard) and a photometer (Gamma Model 700). The spectroradiometer was used to measure the spectral irradiance produced by the sources at full lamp output but the treatment levels of irradiance were below the sensitivity of the spectroradiometer. Absolute measurements of light intensity were made 25 cm above the water surface (the difference between this position and within the water would be < 10%). The light treatments were varied by placing neutral density filters in each of the light sources; the neutral density filters were calibrated on an optical bench. Test levels we used were computed from the filter factors for the neutral density filters. The photometer was used to check irradiance levels prior to a test, but we believe the computed values to be more accurate. Irradiance distribution in the tank was mapped using the photometer and the treatment values weighted by tank area so that they represented the average irradiance 25 cm above water surface.

Our laboratory estimates of the visual threshold for schooling were used to calculate the maximum possible depth of schooling in the sea for various levels of incident irradiation and water types. Threshold values in W cm^{-2} were converted to anchovy effective units (W cm$^{-2}_{\text{anch. eff.}}$) by weighting the spectrum in the apparatus by the relative sensitivity of the scotopic curve of the anchovy *Engraulis encrasicholus* from an electroretinogram by Protasov (1964) (Table 1). Two levels of night illumination were used, full moon at 3 m depth (2.78×10^{-9} W cm^{-2}), and starlight at the earth's surface (1.08×10^{-10} W cm^{-2}) (both measurements from Munz and McFarland 1977). The depth (meters) in the sea (Z) at which a given threshold (E_z) value occurred was calculated using the equation of Baker and Smith (1982):

$$Z = \frac{\ln\left(\dfrac{E_z}{E_0}\right)}{-K_f}$$

where E_0 is the incident radiation (full moon or starlight) in anchovy effective units. K_f is the wave length specific attenuation coefficient and is the sum of coefficients for pure water (K_w), dissolved organic matter (K_d), and chlorophyll a (K_c). Tables of coefficients, and equations for calculating these attenuation coefficients, are given by Baker and Smith (1982). In our calculations we assumed that the dissolved organic matter was constant at 0.7 mg l^{-1} which is typical of the anchovy habitat. We calculated K_c for a range of chlorophyll (Chl) a concentrations ranging from 0.1 to 10 mg Chl a m^{-3} and at 25 nm intervals from 425 to 600 nm for each Chl a concentration. Each K_f value for 25 nm increments was weighted by the appropriate anchovy scotopic sensitivity, and the average anchovy weighted $K_{f\ \text{anch. eff.}}$ was used in the final calculation of Z.

Many uncertainties and possible biases exist in such an extrapolation from laboratory to sea conditions: Cloud cover was not considered nor were possible effects of bioluminescence; spectral irradiance values for full moon and starlight of Munz and McFarland (1977) may not be representative of conditions in the anchovy habitat although they are relatively close to those given in photometric units by Brown (1952); variation in dissolved organic matter is not considered; the radiance distribution over 360° in the tank probably does not resemble that in the sea (only downwelling irradiance was considered here); use of the action spectrum based on an electroretinogram of a dark adapted *E. encrasicholus* eye instead of one for schooling of *E. mordax*; and of course, the usual statistical uncertainties. Despite these uncertainties and biases we believe our estimates of schooling depth are the most accurate to date thanks to the models developed by Baker and Smith (1982).

RESULTS AND DISCUSSION

The schooling threshold based on the index of dispersion was between 4.8×10^{-12} and 7.8×10^{-10} W cm^{-2} (Fig. 1; Table 2). At the lower value and in darkness the index of dispersion ($s^2/\bar{x}$ fish per

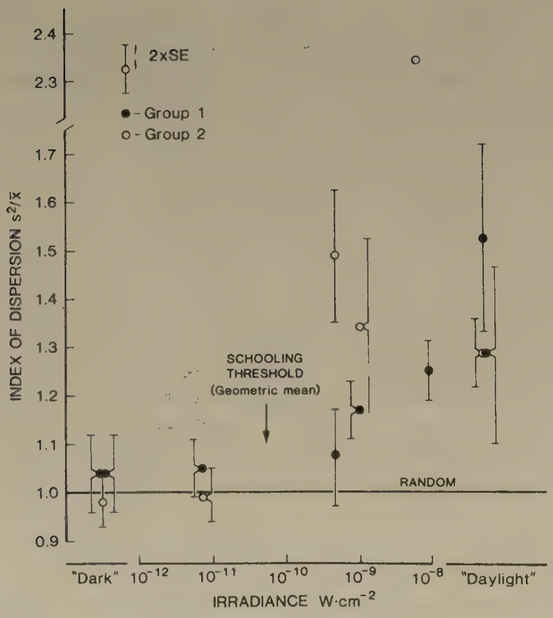

FIGURE 1.–Visual threshold for schooling in northern anchovy. Schooling is indicated by the index of dispersion ($s^2/\bar{x}$). A ratio of 1 implies no schooling as it indicates a random distribution. Each point is a mean calculated from 8-10 photographs and bars are ± 2 × standard error of the mean. No error bars are given for one value (2.34 ± 0.47) because it falls far beyond the rest of the values. Mean dispersion is shown for four test levels of downwelling irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" (1.496×10^{-5} W cm^{-2}) which was the normal daytime level of irradiance in the apparatus.

quadrat) did not differ from unity indicating that the fish were randomly distributed. Hence no schooling existed at the lower irradiance value and in darkness, whereas at the higher value the fish were clearly aggregated. These values delimit a region of about 2 log units of irradiance where one cannot be certain if schooling occurs or not. The actual threshold for schooling must fall somewhere in that region, and we have arbitrarily considered the threshold value to be the geometric mean irradiance of the above two irradiances (6×10^{-11} W cm^{-2}) thereby reducing the uncertainty in the threshold value to about 1 log unit. In subsequent tables and figures we give the upper and lower bounds of the region as well as the threshold value, however.

The variance of the dispersion index, a measure of the variation in school dispersion among photographs, increased sharply at irradiances above the threshold indicating a wide variation in the dispersion of fish among photographs. This can be expected because schooling fish react to fright stimuli, feeding, and many other conditions by altering interfish distances, thereby changing the cohesion or degree of dispersion of the school (Blaxter and Hunter 1982). At light levels below the visual threshold, fish are unable to respond socially to such stimuli, hence the variation among photographs is low.

Mean distance to the nearest neighbor followed the same pattern as we have described for the index of dispersion. Values in darkness and at the lower

TABLE 2.—Mean and standard deviation of the index of dispersion and mean distance to the nearest neighbor for various irradiance levels.

		Schooling indices				
		Dispersion index ($s^2/\bar{x}$)		Mean distance to nearest neighbor (cm)		
Irradiance (W cm^{-2})	Group	$\bar{x}$	s	$\bar{x}$	s	Number of photographs
1.496×10^{-5} ("daylight")[1]	1	1.28	0.29	17.50	3.71	10
	1	1.52	0.30	12.15	4.10	10
	2	1.28	0.11	24.61	4.94	10
[2]8.92×10^{-9}	1	1.25	0.10	12.19	2.52	10
	2	2.34	0.74	19.49	5.50	10
[2]1.079×10^{-9}	1	1.17	0.09	16.65	3.86	10
	2	1.34	0.27	21.72	7.14	10
[2]4.777×10^{-10}	1	1.07	0.15	18.48	3.86	9
	2	1.49	0.21	18.05	6.62	10
[2]7.785×10^{-12}	1	1.05	0.09	21.87	5.39	8
	2	0.99	0.07	30.40	5.14	10
Dark[3]	1	1.04	0.12	21.20	4.16	9
	1	1.04	0.12	19.61	4.83	9
	2	0.98	0.07	34.12	6.36	10

[1] Unfiltered tungsten lamp.
[2] Filtered lamp - spectrum given in Table 1.
[3] Below sensitivity of 931A photomultiplier.

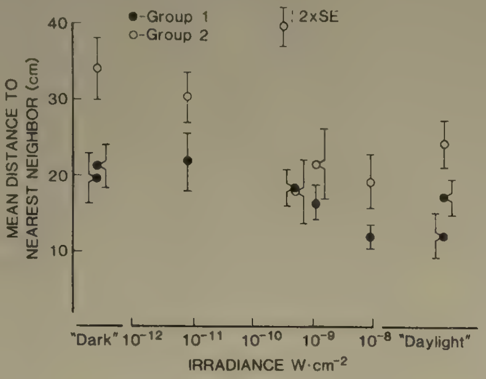

FIGURE 2.–Visual threshold for schooling in northern anchovy is indicated by changes in the mean distance to nearest neighbor. Each point is a mean calculated from 8-10 photographs and bars are ± 2 × standard error of the mean. Mean distance to the nearest neighbor is shown for four test levels of irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" (1.5 × 10^{-5} W cm^{-2}) which was the normal daytime level of irradiance in the apparatus.

irradiance values were not statistically different. Above the threshold the mean distance to nearest neighbor was lower than that in darkness indicating closer spacing among pairs, but no trend with light intensity seemed to exist above the threshold range (Fig. 2). For the purpose of estimating a threshold, however, we believe the index of dispersion is preferable because the criterion for randomness is well defined and the dispersion index takes into account all 50 fish, whereas we used only 10 random pairs per photograph for the nearest neighbor measurements which reduced its precision.

Our calculations indicate that in water of low chlorophyll concentration (0.2 mg Chl a m^{-3}) the threshold irradiance for schooling occurs at a depth of 38 m during a full moon and at a depth of 30 m on a starlit night (Fig. 3). The method of calculation is described in the Methods section on radiometric procedures. Light attenuates rapidly as Chl a concentration increases up to about 2 mg m^{-3} total chlorophyll; at 2.0 mg Chl a m^{-3} the schooling threshold occurs at a depth of only 8 m on a starlit night and at 20 m under full moonlight. Above 2 mg Chl a m^{-3} light attenuates more slowly with increasing Chl a concentration with the threshold at 10 mg Chl a m^{-3} falling at 5 m in starlight and at 12 m in full moonlight. These calculations indicate that sufficient light exists at night for northern anchovy to school within the upper 10 m of nearly all habitats under clear skies, but the maximum possible depth of the schooling would be expected to vary greatly with water type and incident light intensity. An order of magnitude decline in incident irradiation can be expected under the darkest storm clouds (Brown 1952); under these conditions schooling may not be possible at the highest chlorophyll concentrations.

It seems appropriate to use these visual thresholds as estimates of the maximum depth of spawning because spawning probably also depends upon the ability of anchovy to see one another. We calculated the vertical distribution of newly spawned anchovy eggs (0-4 h old, type "S") using data from the unpublished vertical distribution study of Pommeranz and Moser (1983). We selected sets of vertical samples at two stations for which surface Chl a concentrations had been measured and then calculated a mean Chl a concentration for an inshore and offshore series of net hauls. We then estimated the maximum depth for schooling assuming that the surface Chl a was equivalent to an integrated value for the water column as required by the Baker and Smith 1982 model. Spawning occurred closer to the surface at the inshore station which had a high Chl a concentra-

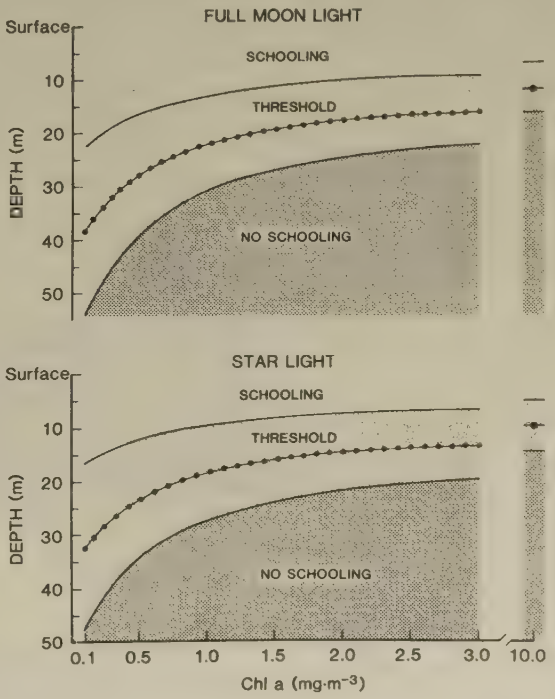

FIGURE 3.–Maximum depth of schooling of northern anchovy in waters of various chlorophyll concentrations (Chl a) under starlight and full moon. Coefficients used in calculations are in Table 1 and in Methods section. Darkly shaded area indicates proportion of water column where no schooling is expected, lightly shaded area indicates depth range of schooling threshold. Central dotted line is the geometric mean.

tion (1.5 mg m^{-3}) than at the offshore station which had a lower concentration (0.24 mg Chl a m^{-3}). At the onshore station only 4% of the eggs occurred below 20 m, whereas at the offshore station 31% were below 20 m. This difference is particularly striking because the inshore samples were taken under a full moon, whereas the moon was in the first quarter when the offshore station was occupied. At both stations the predicted maximum depth for schooling was close to the observed maximum depth for newly spawned eggs (Fig. 4). We may have underestimated the depth of schooling for the offshore (low Chl a) station as we used a starlight value of Munz and McFarland (1977) because no data existed for 1/4 moon. Spawning occurred prior to moonset since spawning occurs between the time of 1800 and 2400 and moonset varied from about the time of 2130 to 0200 (19-25 March 1980). In addition, the offshore station had a deeper mixed layer (about 35 m) than the inshore station (about 10 m) and vertical distribution of anchovy eggs and larvae also may be affected by the depth of the mixed layer (Ahlstrom 1959). Regardless of these uncertainties, these data indicate that underwater visibility may set the maximum depth for spawning of anchovy, although other factors, such as low temperature, might constitute an additional barrier to spawning schools. Thus fish visual thresholds may be a convenient way to establish a general function for estimating the maximum depth of spawning for anchovy and perhaps other pelagic spawning clupeoids in all habitats. Such a general function, that could account for much of the variation in the maximum depth of eggs, could be quite useful in three dimensional models of larval transport or predation. A spawning-depth, water-type function based on visual thresholds seems particularly attractive owing to the considerable cost of accurately measuring the vertical distribution of eggs and larvae even in a single habitat let alone the cost for estimating it for all possible spawning habitats of the population.

To compare the northern anchovy schooling threshold to literature values we converted our radiometric measurements to lux or meter candles (mc), by weighting the spectral irradiance in the apparatus by the human photopic curve, as the literature values are largely in photometric units (see reviews by Whitney 1969 and Blaxter 1970). The visual threshold for anchovy schooling (2.6 × 10^{-4} mc, Table 3) is about an order of magnitude higher

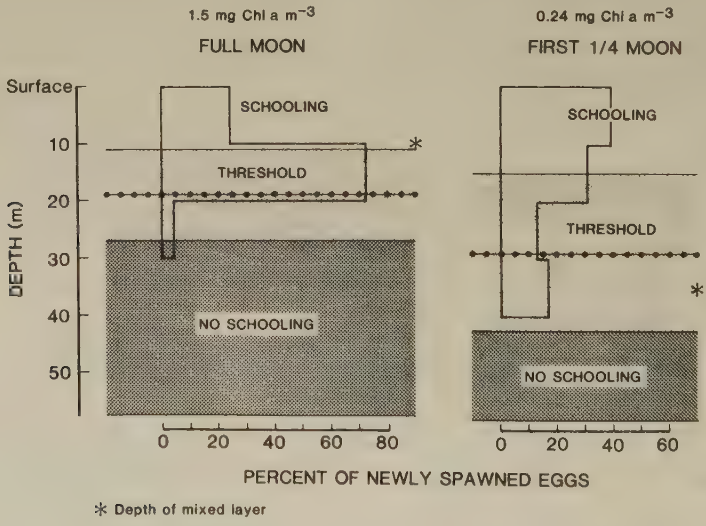

FIGURE 4.–Comparisons of the estimated depths of schooling of northern anchovy and the observed depths of spawning. Estimated depth of schooling calculated from visual threshold estimates (W cm$^{-2}_{\text{anch. eff.}}$), an assumed dissolved organic matter of 0.7 mg l^{-1}, and the average Chl a concentration and moon phase at the station (1/4 moon phase assumed to be equivalent to starlight) using the model of Baker and Smith (1982). Observed spawning depths at the two stations are indicated by a frequency histogram for newly spawned anchovy eggs where the y axis indicates the depth stratum of the plankton tow and the x axis indicates the percentage of newly spawned eggs taken at each of the 10 m vertically stratified tows. Data are from Pommeranz and Moser (1980) and are for the total number of newly spawned eggs taken over a 4-8 d interval.

TABLE 3.—Upper and lower bound and geometric mean for the visual threshold for schooling of adult northern anchovy, *Engraulis mordax*, in the various energy units.

Energy units	Schooling[1]	No schooling[2]	Geometric mean[3]
Radiometric ($W\ cm^{-2}$)	4.777×10^{-10}	7.785×10^{-12}	6.051×10^{-11}
Anchovy effective[4] ($W\ cm^{-2}{}_{anch.\ eff.}$)	3.079×10^{-10}	5.018×10^{-12}	3.900×10^{-11}
Photometric[5] (mc)	2.048×10^{-3}	3.337×10^{-5}	2.594×10^{-4}

[1] Lowest irradiance level at which schooling occurred.

[2] Highest irradiance level at which anchovy failed to school.

[3] Geometric mean of the irradiance at the upper and lower bounds of the threshold.

[4] Weighted by ERG action spectra for *Engraulis encrasicholus* dark adapted retina (413-612 nm) (Protasov 1964).

[5] Weighted by the 1964 human photopic response (413-600 nm).

than that for jack mackerel (3.5×10^{-5} mc, Hunter 1968), a species associated with anchovy in the California Current. Visual thresholds for schooling in fishes range from about 1×10^{-5} to 1×10^{-1} mc with about 90% (14/16) of the literature values being higher than anchovy (Blaxter 1970). We do not attach much importance to such specific differences because criteria for schooling differ widely and radiometric procedures in the older studies were primitive by today's standard. We suspect the threshold for jack mackerel may have been lower than the northern anchovy because of use of a uniform and highly reflective background in the apparatus and the use of photometric brightness as a unit of measurement. In our work the brightness to the sides and below was much lower than the downwelling irradiation whereas this was not the case in the jack mackerel experiment.

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull., 60:107-146.

BAKER, K. S., AND R. C. SMITH.
1982. Bio-optical classification and model of natural waters. 2. Limnol. Oceanogr. 27:500-509.

BLAXTER, J. H. S.
1970. 2. Light 2.3 Animals 2.32 Fishes. *In* O. Kinne (editor), Marine Ecology, Vol. 1, Part 1, p. 213-320. Wiley-Interscience, Lond.

BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20:1-223.

BROWN, D. R. E.
1952. Natural illumination charts. U.S. Navy Bur. Ships Project NS 714-100, Rep. No. 374-1, Wash., D.C., 11 p.

HUNTER, J. R.
1966. Procedure for analysis of schooling behavior. J. Fish. Res. Board Can. 23:547-562.
1968. Effects of light on schooling and feeding of jack mackerel, *Trachurus symmetricus*. J. Fish. Res. Board Can. 25:393-407.

HUNTER, J. R., AND C. A. KIMBRELL
1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 78:811-816.

LOUKASHKIN, A. S.
1970. On the diet and feeding behavior of the northern anchovy, *Engraulis mordax* (Girard). Proc. Calif. Acad. Sci., Ser. 4, 37:419-458.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game, Fish Bull. 162, 79 p.

MUNZ, F. W., AND W. N. MCFARLAND.
1977. Evolutionary adaptation of fishes to the photic environment. *In* F. Crescitelli (editor), The visual system in vertebrates, Vol. 7 (Part 5), p. 193-275. Handb. Sens. Physiol.

PIELOU, E. C.
1969. An introduction to mathematical ecology. Wiley-Interscience, N.Y., 286 p.

PITCHER, T. J., B. L. PARTRIDGE, AND C. S. WARDLE.
1976. A blind fish can school. Science 194:963-965.

POMMERANZ, T., AND H. G. MOSER.
1983. Vertical distribution study R/V *Ellen B. Scripps* March 19-April 4, 1980. Admin. Rep. LJ-83-01, 368 p.

PROTASOV, V. R.
1964. Some features of the vision of fishes. [In Russ.] A. N. Severtsov Inst. Anim. Morphol., Acad. Sci. U.S.S.R., p. 29-48. Marine Laboratory, Aberdeen, U.K., Transl. No. 949.

SMITH, P. E.
1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar. *In* G. B. Farquhar (editor), Proceedings on biological sound scattering in the ocean, p. 563-600. MC Rep. 005, Maury Cent. Ocean Sci., Dep. Navy, Wash., D.C.

SQUIRE, J. L., JR.
1978. Northern anchovy school shapes as related to problen in school size estimation. Fish. Bull., U.S. 76:443-448.

WHITNEY, R. R.
1969. Schooling of fishes relative to available light. Tran Am. Fish. Soc. 98:497-504.

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Batch Fecundity in Multiple Spawning Fishes

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ABSTRACT

Methods for estimating batch fecundity are described, including identification and sampling the eggs that constitute one spawning batch within the ovary. Using northern anchovy, *Engaulis mordax*, as an example, methods are developed for evaluating the accuracy and precision of batch fecundity estimates. Included in this analysis are the number and location of ovarian tissue samples, optimal numbers of females, and selection of the appropriate function to express the relation between batch fecundity and female weight. We found for anchovy that the optimum number of ovarian tissue samples was 2-3 per ovary and that to keep the coefficient of variation for the mean fecundity of population under 10% required a sample of 50 or more females. Analysis of covariance indicated that the batch fecundity of northern anchovy varied significantly among years (1951-84) indicating that the relation between female weight and fecundity must be newly established each year.

INTRODUCTION

A key issue in the estimation of fecundity of oviparous fishes is whether or not the annual fecundity can be estimated from the standing stock of advanced oocytes in the ovary prior to the onset of the reproductive season. In some boreal species, frequently called total or isochronal spawners, all the eggs to be released in a season develop synchronously prior to spawning (hence the term isochronal) and spawning typically takes place over a short period (Holden and Raitt 1974). In such species, the standing stock of oocytes within a certain range of maturity classes is considered to represent the annual fecundity of the spawner. The groups of oocytes to be spawned in the season are usually identifiable because a distinct hiatus in oocyte maturity classes exists between the small, immature, unyolked oocytes that occur the year around and the synchronously maturing annual batch (Hickling and Rutenberg 1936; Yamamoto 1956). Although some of these fishes may spawn repeatedly during the season, for example, whiting and haddock, the standing stock of yolked eggs is considered representative of the annual fecundity (Hislop 1975; Hislop et al. 1978; Hislop, pers. commun.[1]). An exception to this occurs when unfavorable conditions result in resorption of some of the advanced eggs in the ovary at the end of the season. The extent of this potential bias (overestimation of annual fecundity) is unknown.

In many temperate and tropical fishes (frequently called multiple, partial, serial, or heterochronal spawners), annual fecundity is seasonally indeterminate and batch fecundity is the only useful measurement. In such fishes the standing stock of yolked eggs, regardless of maturity state, give no indication of annual fecundity because these fishes continuously mature new spawning batches throughout a typically protracted spawning season. In the active ovaries of fishes with indeterminate annual fecundity, the oocytes usually occur in nearly all maturity stages; they range in size continuously from small unyolked oocytes <0.1 mm diam. to yolked oocytes 0.4-0.7 mm diam., and no large hiatus exists between maturity classes of oocytes except for one between hydrated oocytes and advanced yolked oocytes which is of a temporary nature. Such fishes usually spawn many times during a season. The northern anchovy spawns at 7-10 d intervals for 2 or 3 mo and averages 20 spawnings per yr (Hunter and Leong 1981), and the scianid, *Seriphus politus*, has a similar reproductive output (DeMartini and Fountain 1981). Thus, for these fishes, identification of a predetermined annual spawning batch is a hopeless exercise, and the only useful fecundity measurement is the number of eggs produced in a single spawning batch (batch fecundity); annual fecundity is a function of both the batch fecundity and the number of spawnings per year. Spawnings are so numerous in these fishes that small unyolked oocytes <0.1 mm diam. would have to mature in a season to account for the number of spawnings (Hunter and Leong 1981).

The standing stock of oocytes is occasionally used to estimate annual fecundity in such common fishes as *Scomber*, *Trachurus*, and *Merluccius*, which by the standard criteria have indeterminate fecundity. That annual fecundity is predetermined in such fishes is an assumption with little or no supporting evidence. The criteria and approaches for distinguishing between determinate and indeterminate fecundity are discussed in greater detail (Hunter and Macewicz 1985).

The objective of this paper is to describe the methodologies for estimating batch fecundity in fishes with indeterminate seasonal fecundity. We do not consider the well documented methodology for fecundity estimation of fishes with seasonally determinate fecundity (see, for example, Holden and Raitt 1974). In anchovy and other fishes with indeterminate annual fecundity, the oocytes in active ovaries are typically distributed in 1-2 modes (Fig. 1), each mode representing a single spawning batch. Maturation of oocytes and vitellogenesis are a continuous cycle: when one spawning batch is spawned, another spawning batch is ready for the last stages of maturation and spawning (Fig. 2). Vitellogenesis proceeds rapidly after a spawning, with the ovary doubling in dry weight during the interval between spawnings (Hunter and Leong 1981). The final stage of maturation, hydration, is characterized by a rapid secretion of fluid of low specific gravity into the advanced eggs by the granulosa cells of the follicle (Fulton 1898). This fluid causes more or less complete fusion or solution of the yolk granules producing the translucent appearance of hydrated eggs. The volume of the egg or wet weight increases three- or four-fold (Fulton 1898), but the increase in dry weight is negligible (LeClus 1979a). In northern anchovy, hydration begins about 12 h before spawning when the eggs are between 0.6 and 0.8 mm (major egg axis) and causes a four-fold increase in wet weight of the ovary as the egg increases to 1.3 mm (major axis) (Hunter and Macewicz 1980; Hunter and Leong 1981) (Fig. 2). Ovulation and spawning soon follow completion of hydration in most clupeoids (anchovy, pilchard, sardines, and others) but in herring, a total spawner, ovulated eggs may be retained in the ovary for an extended period.

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[1] John R. G. Hislop, DAFS Marine Lab., P.O. Box 101, Victoria Road, Aberdeen AB9 8DB, Scotland, pers. commun. Oct. 25, 1983.

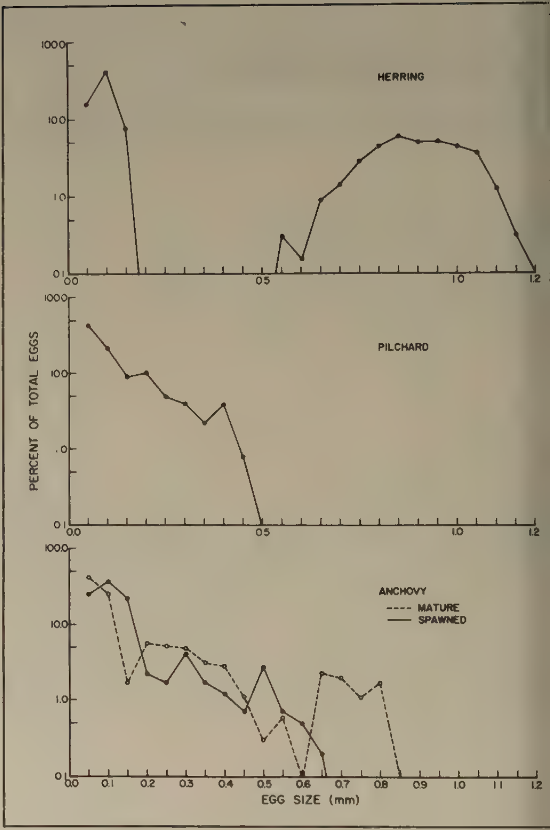

Figure 1.—Frequency distribution of oocyte diameter in the ovaries of herri
pilchard (Hickling and Rutenberg 1936), and northern anchovy (Hunter and Le
1981). Herring spawns a single batch each year; other species are multiple-ba
spawners. In the anchovy, the solid line shows a recently spawned female,
broken line a female about to spawn (just before hydration of the oocytes). (Fr
Blaxter and Hunter 1982.)

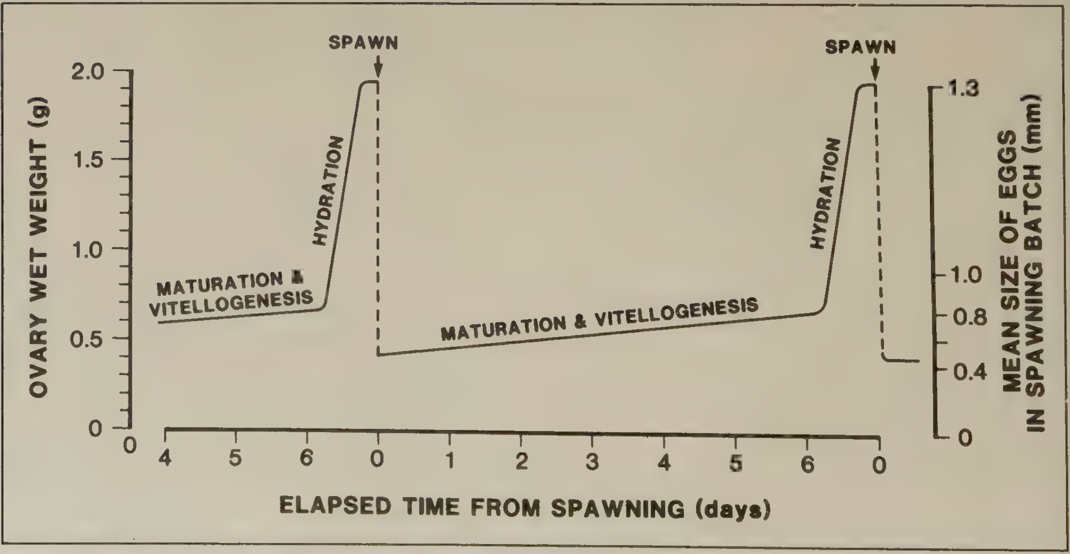

Figure 2.—Maturation cycle of a 12.5 g northern anchovy female during peak spawning months where the average interval between spawnings is 7 d. The change in mean wet weight of the ovary is indicated on the left axis and the mean diameter of the oocytes in the most advanced spawning batch on the right axis. Data from Hunter and Goldberg (1980) and Hunter and Macewicz (1980).

LABORATORY PROCEDURES

Identifying and Counting Oocytes in a Batch

A number of criteria have been used to identify the oocytes to be included in a spawning batch. These include 1) counts of all yolked oocytes; 2) estimation of the number of oocytes in the most advanced spawning batch by measuring the size distribution of oocytes in the ovary and identifying the most advanced (largest) modal group of oocytes; and 3) estimation of the number of oocytes in a spawning batch by counting the number of hydrated oocytes.

The first method can be rejected because the standing stock of yolked oocytes gives indication neither of total fecundity nor of batch size in fishes with indeterminate fecundity and is appropriate only for fishes with determinate seasonal fecundity. The second method (oocyte size frequency) usually gives results similar to those based on counts of hydrated oocytes if females with highly advanced oocytes are used (Hunter and Goldberg 1980; Laroche and Richardson 1980). We believe the third method, counting the hydrated oocytes, is preferable because it requires less time and avoids the problem of partitioning oocytes between the most advanced mode and the adjacent group of smaller oocytes. Before describing methods 2 and 3, it is important to consider methods of sampling the ovary.

Methods of Sampling an Ovary

It is impractical to count and measure all advanced oocytes, or to count all hydrated oocytes in an ovary, owing to the great fecundity of most marine fishes. Thus, regardless of the method used for identifying the spawning batch, ovarian subsamples are required, and these are related to either the ovarian weight (gravimetric method) or the total volume of an aqueous suspension of all oocytes in the ovary (volumetric method). The gravimetric method is based on counting oocytes in weighed samples of ovarian tissue and relating the tissue samples to the total ovary weight. In the volumetric method, the ovary is preserved in Gilson's fluid which frees the oocytes from the ovarian tissue by breaking down the connective tissue (see Baganel 1967 for the recipe for Gilson's fluid). The released oocytes are cleaned, put in a volumetric cylinder filled to a known volume with water, shaken to provide thorough mixing, subsamples of known volume are withdrawn using a Stempel pipette, and the oocytes staged and counted (Holden and Raitt 1974). Automatic oocyte counters may also be employed.

The volumetric method may be used for batch fecundity estimation if the eggs constituting the batch are identified using the egg size-frequency method; however, the volumetric technique is inappropriate if the hydrated oocyte method is used because Gilson's fluid destroys hydrated eggs. Substantial shrinkage of oocytes occurs when ovaries are preserved in Gilson's fluid; an average shrinkage of 24% (compared to formalin-preserved ovaries) occurs when skipjack and yellowfin tuna ovaries are preserved in Gilson's fluid, but no differential shrinkage occurs among oocyte size classes (Joseph 1963). Thus, to make oocyte size classes comparable to live, or formalin-preserved, or histological sections, the extent of shrinkage must be measured and the data corrected. Treatment with Gilson's fluid also destroys the ovary, making histological analysis impossible.

We use the gravimetric method of MacGregor (1957), which is somewhat similar to the gravimetric method "B" of LeClus (1977) who evaluated two gravimetric and one volumetric techniques. Although LeClus obtained very low coefficients of variation for all techniques in her 1977 methods paper, the relative fecundity estimated for the South African anchovy in a subsequent paper (LeClus 1979b) was as variable as those employing less complicated procedures (MacGregor 1957, 1968; Hunter and Goldberg 1980). Her use of vacuum dry weight of the ovary, instead of formalin wet weight, seems an unnecessary refinement. Natural variability in batch fecundity appears to be much greater than the variation caused by differences in the technique of sampling the ovary.

The step-by-step procedure for the hydrated oocyte method is outlined below. It will be elementary to many biologists, but it is intended as a guide for inexperienced staff. Except for some details outlined in a subsequent section, the same procedure can be used to estimate batch fecundity using the oocyte size-frequency method.

The Hydrated Oocyte Method

1. The basic method is as follows: Numbers of hydrated oocytes in weighed tissue samples of formalin-preserved ovary are counted and the counts are then projected to estimate numbers of hydrated oocytes in the entire ovary which is assumed to be equivalent to batch fecundity.

2. Prior to batch fecundity estimation, females are accurately weighed, and the ovary removed, weighed, and stored in an individual vial of buffered 10% formalin. Ovaries which appear hydrated are noted along with an estimate of the numbers of free eggs in a collection jar (Hunter 1985). Only hydrated ovaries which have not lost oocytes are used for fecundity estimation; ovaries that have lost oocytes in the jar are rejected after histological examination because they contain postovulatory follicles.

3. Needed supplies and equipment include a balance sensitive to 0.1 mg (which should be checked with standard weights), a dissection microscope with a 10× objective, hand counter, forceps, scalpel, bottle of glycerin (33% glycerol solution by volume) with eyedropper, glass slides (25×75 mm), cover slips (22×50 mm), paper towels for blotting, and weighing paper.

4. Remove ovary from the formalin fixative and blot dry with paper towel. Break the ovarian membrane and remove three tissue samples of the ovary. The ovary is soft and the sample can be removed easily with the tip of the forceps or scalpel. Remove samples from positions about one-third of the distance from each end of the ovary to insure that no two samples come from the same portion of the ovary (only one ovary, left or right, need be used). Try to obtain a tissue weight of 30-50 mg, as this will contain an adequate number of hydrated oocytes (100-200). Place sample on a preweighed piece of weighing paper and record weight to nearest 0.1 mg. Pieces of ovary can be added or removed to vary sample weight.

5. Place the sample on a slide and cover with 3-4 drops of glycerin. After 10-15 min, loosen the oocytes by gently tapping the piece of ovary with the blunt tip of the forceps. After the oocytes are loosened, add 3 or 4 more drops of glycerin, spread the sample over the slide, and cover with a cover slip so that it floats on the fluid. (We found that this concentration of glycerin had no effect on the diameters of oocytes taken from formalin-preserved ovaries, even after 24 h.)

6. Place the slide under the microscope, and with a hand counter tally the number of hydrated oocytes in the sample. Hydrated oocytes can be distinguished easily from other oocytes by their large size

(usually ≥0.8 mm in the major axis in northern anchovy), wrinkled appearance when formalin preserved (yolked but nonhydrated oocytes usually retain their smooth surface contour), and by their translucence (nonhydrated eggs are relatively opaque, Fig. 3). Some damage to the hydrated oocytes may occur during slide preparation. In some cases, the chorion may be ruptured and the yolk extruded. Do not count empty chorions, and count only those fragments judged to be major portions of the oocytes.

7. Batch fecundity (*Y*) for each female is calculated from the product of the number of hydrated oocytes (eggs) per unit weight in the tissue sample and the ovary weight (left and right sides combined) (*Z*).

8. The egg production method requires that batch fecundity be expressed as a function of female weight and not length, i.e., $EY = f(w)$ where female weight (*w*) is the formalin wet weight of the female without the ovary (formalin wet weight can be converted to live weight using coefficients given in Hunter 1985). We use ovary-free wet weight of females since females with hydrated ovaries temporarily have a higher weight than the average female because of the increased weight of the hydrated ovary. The ratio of female body weight without ovary to female weight with ovary (excluding females with hydrated or immature ovaries) can be used to convert ovary-free wet weight to total body weight. This ratio in northern anchovy was 0.95 for female anchovy taken 1978-79 (Hunter and Macewicz 1980).

Oocyte Size-Frequency Method

If the number of females with hydrated oocytes is insufficient for a batch fecundity estimate, the more time-consuming oocyte size-frequency distribution method can be employed (MacGregor 1957). This method takes 1-3 h per fish (3 tissue samples per fish) as compared with 1-1.5 h for the hydrated oocyte method. In this method, a size-frequency distribution of oocytes is constructed and the most advanced modal group of oocyte size classes (the mode composed of the largest oocytes) is determined by inspection. The total number of oocytes within the oocyte size classes that constitute the advanced modal group is considered to be the spawning batch. This method usually gives results similar to those based on counts of hydrated oocytes if females with highly advanced oocytes are used (Hunter and Goldberg 1980; Laroche and Richardson 1980). The mean size of the group of oocytes that constitutes the most advanced spawning batch should be ≥0.5 mm, as estimates of batch fecundity are somewhat inflated if a less mature ovary is used (Hunter and Goldberg 1980).

In northern anchovy, a tissue sample weight of ≤10 mg will insure that about 100 oocytes are included in the most advanced modal group of oocytes. All oocytes ≥0.3 mm in a tissue sample are counted using a set of hand counters and measured to the nearest 0.05 mm. We use an optical comparator at 50× magnification and measure the oocytes with a rule on the viewing screen of the comparator. A starting oocyte size ≤0.3 mm is recommended to insure that a

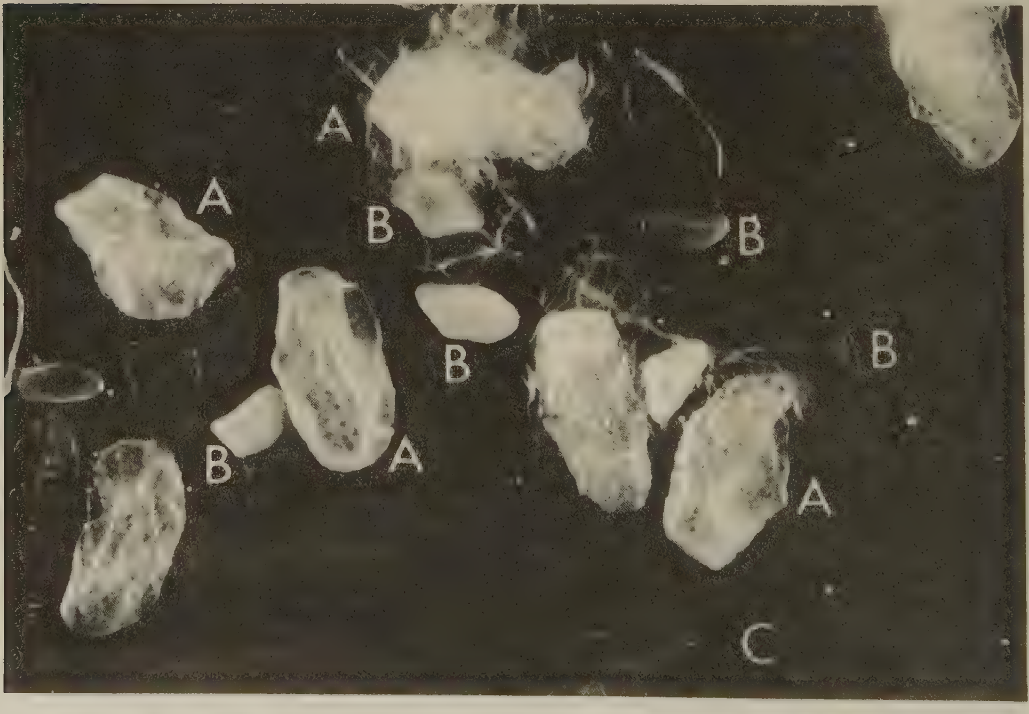

Figure 3.—Hydrated oocytes in a tissue sample taken from a northern anchovy ovary preserved in formaldehyde solution. A. Hydrated oocytes; B. Unyolked and yolked oocytes (before hydration); C. Empty chorion of a hydrated oocyte (the chorion, or a major fragment of it, would be included in the count of hydrated oocytes for the batch fecundity estimate). These hydrated oocytes were 1.2 mm long in the major axis.

sufficient number of 0.05-mm oocyte size classes exist below the most advanced modal group. Inclusion of these small oocyte size classes insures an accurate separation of the tail of the advanced mode of oocytes from the smaller oocytes adjacent to it. To separate the tail of the advanced modal group from the adjacent group of smaller oocytes, we use probability paper analysis (Harding 1949; Cassie 1954). In other respects, the oocyte size-frequency method is the same as the hydrated oocyte method, and the previous section can be used as a guide.

ACCURACY AND PRECISION

In this section we develop methods to evaluate the accuracy and precision of estimating batch fecundity using the hydrated egg methodology, and apply these procedures to northern anchovy fecundity data. Accurate estimation of batch fecundity depends upon selection of an unbiased location for the samples of ovarian tissue and the selection of an appropriate regression model to express the relation between female weight and batch fecundity. The precision of the estimate depends upon the number of ovarian tissue samples taken per female and the total number of females. The weight of the individual tissue sample also affects precision, but we have not considered this element. We have instead kept the tissue samples within a weight range that yields about 100-200 hydrated oocytes per sample.

In the first subsection we use analysis of variance to detect the possible effects of location of tissue samples within the ovary. In this analysis we use a sample of 12 northern anchovy ovaries in which 6 tissue samples were taken per ovary at specified locations. In the next subsection we determine how the number of tissue samples affect the precision of the fecundity estimate; consider various fecundity-weight models; and determine the optimum numbers of fish and tissue samples for a given cost. For this analysis we add an additional 12 fish to the sample used in the first section, all of which had 6 tissue samples per fish. In the third subsection we use seven data sets on anchovy batch fecundity taken 1951-60 and 1978-84 (n ranges, 19-127) to validate selection of the fecundity-female weight model and to assess the precision of regression estimates of batch fecundity. In the final subsections we consider how the number of fish in the sample affects precision of the fecundity estimate and how the batch fecundity varies among years.

Location of Tissue Samples Within the Ovary

To determine if location of the tissue samples affects estimates of batch fecundity in anchovy, we took 6 ovarian tissue samples from each of the 12 ovaries; three samples were taken from the left ovary and three from the right. In each set of three, one sample was taken in the center and the other two were about one-third of the distance from each end of the ovary. The number of eggs per unit weight of the ovary (x) was calculated for each tissue sample. We tested effects of right or left ovarian side, and position of tissue samples within a side, using the two-way analysis of variance. The natural logarithm of x was used in the analysis because there is a positive correlation between the same sample mean and its standard deviation. The assumption of homogeneity within sample variance is violated when the means differ.

No difference existed either in the location of the tissue sample within right or left sides of the anchovy ovary or between right and left sides (Table 1). Thus in northern anchovy, tissue samples can be taken from any location or from either the right or left sides. It should be noted, however, that all of our samples were of females taken at a time of day (1900-0100 h) when hydration was nearly complete. If females are taken earlier in the day, position effects may be likely because hydration does not proceed at a uniform rate throughout the ovary; rather it begins at the periphery and spreads to the central section of the ovary, producing larger hydrated oocytes (more mature) at the periphery than in the center. Thus the number of hydrated oocytes per gram of ovary may be higher in the central section and lower on the periphery at early stages of hydration. Variation in extent of hydration does not appear to be a major source of error, but it should be evaluated prior to making a fecundity estimate in a new species or when samples are taken at a new time of day.

Table 1.—Effect of location of ovarian tissue samples from northern anchovy on the number of hydrated eggs per unit sample weight (g). Effects evaluated by taking tissue samples (n = sample size) from three positions (two ends, I and III, and middle, II) from both the right and left ovary. Analysis of variance indicates insignificance of either side or position within a side (SS = sum of squares; MS = mean square).

Positions of sample in ovary	Mean no. of eggs/g of ovary tissue								
	Right ovary			Left ovary			Both ovaries		
	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n
I	5,237	740	12	5,143	1,158	12	5,190	950	24
II	4,919	790	12	5,243	831	12	5,081	810	24
III	5,296	1,005	12	5,540	2,019	12	5,418	1,564	24
All	5,151	845	36	5,309	1,396	36			

Two-way analysis of variance of eggs/g of ovary tissue.

SS due to	df	SS	MS	F
Right vs. left ovary	1	0.0053	0.0053	0.14
Position within ovary	2	0.0268	0.0134	0.34
Interaction	2	0.0269	0.0134	0.34
Error	66	2.5854	0.0392	—
Total	71	2.6444	—	—

Optimum Number of Tissue Samples and Numbers of Fish for Fecundity Estimation

In this section we develop equations to estimate the optimum number of fish and tissue samples to be used for fecundity estimation using data on the northern anchovy. The precision of the sample variance (or mean square error) around the regression of batch fecundity on female weight (σ_A^2) (a measure of the goodness of fit of the fecundity-weight model) was used to determine the optimum number of tissue and fish samples. This procedure required a definition of a general fecundity model and development of functions to express the error terms.

A. The general fecundity model—The true batch fecundity (Y) where all eggs are counted, and the fish weight relationship (w) is defined as:

$$Y_w = f(w) + A \tag{1}$$

where the error term (A) has a mean = 0, and variance = σ_A^2. Y and Y_w are interchangeable in later sections. Since all the hydrated eggs in a batch (Y) are not counted, $f(w)$ are fitted to the estimated batch fecundities ($\hat{Y}$) calculated from m ovarian tissue samples per fish.

Let's denote for the ith fish, $i=1,\ldots,n$:

w_i = gonad-free fish weight = fish weight minus gonad weight
Y_i = total number of hydrated eggs in the ovary
y_{ij} = hydrated egg count in the jth tissue sample $j=1,\ldots,m$
z_{ij} = weight of jth tissue sample
Z_i = formalin wet weight of gonad
m = number of tissue samples from an ovary
M_i = maximum number of tissue samples in an ovary
$\hat{Y}_{ij}$ = estimated total number hydrated eggs in the ovary from the jth tissue sample = $(y_{ij}/z_{ij})Z_i$
$\hat{Y}_i$ = estimated total number of hydrated eggs in the ovary $= \sum_{j=1}^{m} \hat{Y}_{ij}/m$
$\bar{Y}$ = sample mean number of hydrated eggs $= \sum_{i} \hat{Y}_i/n$
$\hat{\hat{Y}}_i$ = estimate of batch fecundity from the regression model.

Suppose $\hat{Y}_{ij}$ is an unbiased estimate of Y_i, then

$$\hat{Y}_{ij} = Y_i + \hat{Y}_{ij} - Y_i = f(w_i) + A_i + e_{ij} \tag{2}$$

where $e_{ij} = \hat{Y}_{ij} - Y_i$ is the within-ovary error term and is assumed normally distributed with mean = 0 and variance = σ_e^2. Using Equation (2) and the fact that

$\hat{Y}_i = \sum_{j=1}^{m} \hat{Y}_{ij}/m$, we have

$$\begin{aligned}\hat{Y}_i &= f(w_i) + A_i + e_{i.} \\ &= f(w_i) + \xi_i\end{aligned} \tag{3}$$

where $\xi_i = A_i + e_{i.}$ and $\sigma_{\xi_i}^2 = \sigma_A^2 + \dfrac{M_i - m}{M_i}\,\dfrac{\sigma_e^2}{m}$.

Thus the variance around the regression line based upon data set $(\hat{Y}_i, w_i)$ is composed of two variance components: One is σ_A^2 and the other is σ_e^2, the within-ovary variance. The unbiased estimates of $\sigma_{\xi_i}^2$ and σ_e^2 are

$$s_{\xi_i}^2 = \frac{\sum_{i=1}^{n} [\hat{Y}_i - f(w_i)]^2}{n - q} \tag{4}$$

and $$s_e^2 = \frac{\sum_i \sum_j (\hat{Y}_{ij} - \hat{Y}_i)^2}{n\,(m-1)}\,. \tag{5}$$

The parameter q is the number of regression coefficients in the model and n is the number of fish sampled. Most if not all fecundity regressions use only two coefficients (Bagenal 1967) and consequently we use $q = 2$ in this article, and subsequent computations should be redone if $q>2$. For simplicity, we assume that $M_i = M_j = M$ for $j \neq i$, and $\sigma_{\xi_i}^2 = \sigma_{\xi_j}^2 = \sigma_\xi^2$.

Thus $$\sigma_A^2 = \sigma_\xi^2 - \frac{M-m}{M}\,\frac{\sigma_e^2}{m}$$

and $$s_A^2 = s_\xi^2 - \frac{M-m}{M}\,\frac{s_e^2}{m}\,. \tag{6}$$

The variance of the sample variance (s_A^2) is used in the next section for computing the optimum number of ovarian tissue samples for fecundity estimation.

B. Optimum number of tissue samples—Since the goodness of fit of any model is measured by s_A^2, we chose to minimize the variance of s_A^2 with respect to the number of tissue samples (m) for a fixed total cost function (Scheffé 1959).

$$c = c_1 n + c_2 mn \tag{7}$$

where c is the total funds available,
c_1 is the cost of processing a fish, and
c_2 is the cost of processing a tissue sample.

Under the assumption of normality of the error terms, one obtains the variance of s_A^2 as:

$$var\,(s_A^2) = 2\,\sigma_A^4 \left[\frac{\left\{1 + \left(\frac{1}{m} - \frac{1}{M}\right)\theta\right\}^2}{(n-q)} + \left(\frac{1}{m} - \frac{1}{M}\right)^2 \frac{\theta^2}{n\,(m-1)} \right] \tag{8}$$

where $\theta = \dfrac{\sigma_e^2}{\sigma_A^2}$ and $\hat{\theta} = \dfrac{s_e^2}{s_A^2}$.

The optimum sample sizes for selected parameter values are listed in Table 2. The optimum tissue sample size (m) depends on the values of each of the five parameters, i.e., q, $\theta = \sigma_e^2/\sigma_A^2$, c, c_1, and c_2.

Table 2.—Optimum number of ovarian tissue samples required for batch fecundity estimation of northern anchovy with two regression coefficients (q=2) and maximum tissue samples >30 within an ovary (M>30) for various degrees of data variability ($\theta=\sigma_e^2/\sigma_A^2$) and cost constraints ($c/c_2$ and c_1/c_2).

Ratio of within-ovary variance to variance about the line ($\theta=\sigma_e^2/\sigma_A^2$)	Total funds available for estimated cost per tissue sample (c/c_2)	Relative index of processing costs (costs of fish/cost of sample (c_1/c_2)*		
		0*	4	8
θ = 0.5	50	2	2	2
	200	2	3	3
	10,000	2	3	3
θ = 1	50	2	3	3
	200	2	4	4
	10,000	2	4	5
θ = 2	50	3	4	4
	200	3	5	6
	10,000	3	6	7
θ = 3	50	3	5	4
	200	4	7	8
	10,000	4	7	9
θ = 4	50	4	6	4
	200	5	8	10
	10,000	5	9	11
θ = 5	50	5	6	4
	200	6	9	11
	10,000	7	11	13

*0 = case where cost of capturing fish is negligible relative to cost of fecundity estimate.

The finite population correction factor $(1-m/M)$ can be ignored for $M \geqslant 30$. This means that it is unlikely that the finite population correction will ever be used because it is very unlikely that a tissue sample as large as 1/30 of the ovary weight would ever be used in a fecundity estimation. Hence, an infinitely large M ($M \geqslant 30$) can be used for all calculations.

To evaluate the adequacy of Equation (3), we compute a ratio of σ_ξ^2 and σ_A^2, i.e., $K = \sigma_\xi^2/\sigma_A^2$; $K \geqslant 1$. A large K implies the variation in Equation (3) is too high and a larger sample size is desirable. When K is close to 1, the precision of Equation (3) is nearly as good as that of Equation (1) which uses the true fecundity where all eggs in a batch are counted. K is computed from the following equation:

$$K = \frac{\sigma_\xi^2}{\sigma_A^2} = \left(\frac{1}{m} - \frac{1}{M}\right)\theta + 1 \qquad (9)$$

and

$$\hat{K} = \frac{s_\xi^2}{s_A^2} = \left(\frac{1}{m} - \frac{1}{M}\right)\hat{\theta} + 1 \cdot$$

Table 3 gives K values for number of tissue samples ranging from to 6 for $\theta = 0.5\text{-}0.6$. K can be computed easily for other values of θ and number of possible tissue samples within an ovary. The precision of $\hat{K}$ depends on the variance of s_ξ^2 and s_A^2 and the cost function for processing the fish and making the fecundity estimate [Equation (7)]. Costs dictate the number of fish used and the number of tissue samples taken per fish.

To evaluate K for different cost functions (hence sample sizes), t is necessary to select a proper function to express the relationship between fecundity and female weight, $f(w)$. We used four models and the data set of 24 fish (Table 3). The four models were:

$$\hat{Y} = \begin{cases} f_1(w) = aw^b + e \\ f_2(w) = ae^{bw} + e \\ f_3(w) = a + b\ln(w) + e \\ f_4(w) = a + bw + e \cdot \end{cases}$$

The linear model had the greatest precision because it had the lowest s_ξ^2 and s_A^2 (Table 3). The linear model also seems a preferable method of expressing the fecundity-weight relationship in northern anchovy when much larger data sets are considered (see next section).

The parameter $\hat{\theta} = s_e^2/s_A^2$ (a measure of the relative variability within tissue samples) ranged from 0.5 to 0.6, depending on the regression model selected for the 24-fish sample. In our case, the cost (c_1) of catching and curating a single fish is negligible relative to the cost (c_2) of counting the hydrated eggs in a tissue sample because many fish must be taken for the spawning frequency estimation. Thus for northern anchovy, $c_1/c_2 \sim 0$. Using Table 2, the optimum number of tissue samples (m) is 2. For m=2, and $\hat{\theta}$=0.5, $\hat{K}$=1.3 [Equation (9)]. This means that the variance around Equation (3) is about 1.3 times that of the model based on counts of all hydrated eggs in the ovary [Equation (1)]. To reduce the $\hat{K}$ value, more tissue samples are needed which increases the total cost (c). For northern anchovy, there is no reason to increase the number of tissue samples beyond three, because the reduction in $\hat{K}$ becomes negligible at larger sample sizes (Table 3).

Validation of the regression model

In the previous section we concluded that the linear model for expressing the relation of female batch fecundity to female weight was preferable, but we used a small data set (n = 24) in which 3-6 tissue samples were taken per fish. In this section we test and evaluate this conclusion by fitting a linear model ($\hat{Y}_w = \bar{Y} + b(w-\bar{w})$) and two nonlinear models ($\hat{Y} = ae^{bw}$ and $\hat{Y} = aw^b$) to all existing data sets on the fecundity of northern anchovy (1950-84) (Tables 4 and 5). In these sets the number of tissue samples per fish varied from 1 to 3. Mean square error (MSE) $= \Sigma(\hat{Y}-\bar{Y})^2/(n-2)$ was computed for all three models for each data set. Although no apparent difference existed among MSE values for the three models, and no pattern existed in the residuals (Fig. 4), the simple linear model is preferable because: 1) it explains as much variation as the cur-

Table 3.—Effect of ovarian tissue samples taken per ovary (m) on the ratio K for various models that express the relation between female weight, w (without ovary) and batch fecundity, $\hat{Y}_w$.

Regression model $f(w)$	s_ξ^2 ($\times 10^3$)	Maximum no. of tissue samples (M)	$^*s_A^2$ ($\times 10^3$)	$^\dagger s_e^2/s_A^2$	$^\ddagger K$ for 1-6 tissue samples/ovary 1	2	3	4	5	6
(1) aw^b	6,302	∞	5,729	0.60	1.60	1.30	1.20	1.15	1.12	1.10
a = 325.07		80	5,772	0.60	1.59	1.29	1.19	1.14	1.11	1.09
b = 1.2423		30	5,844	0.59	1.57	1.28	1.18	1.13	1.10	1.08
(2) ae^{bw}	7,112	∞	6,539	0.53	1.53	1.27	1.18	1.13	1.11	1.09
a = 3,281.28		80	6,582	0.52	1.51	1.25	1.17	1.12	1.10	1.08
b = 0.0612		30	6,654	0.50	1.50	1.24	1.16	1.11	1.09	1.07
(3) $a+b\ln(w)$	6,274	∞	5,702	0.60	1.60	1.30	1.20	1.15	1.12	1.10
a = −31,831.73		80	5,744	0.60	1.59	1.29	1.19	1.14	1.11	1.09
b = 15,371.04		30	5,816	0.59	1.57	1.28	1.18	1.13	1.10	1.08
(4) $a+bw$	6,220	∞	5,648	0.61	1.61	1.31	1.20	1.15	1.12	1.10
a = 3,190.38		80	5,690	0.60	1.59	1.29	1.19	1.14	1.11	1.09
b = 838.11		30	5,762	0.60	1.58	1.28	1.18	1.13	1.10	1.08

*From equation (6).

†Within-ovary variance (s_e^2) = $3{,}436 \times 10^3$ from Equation (5); ratios computed using 7 digits.

‡K is a measure of the variance around regression line relative to the "free" variance around the curve (Equation (1)). When K = 1, the variance from subsampling ovarian tissue is 0 since all eggs are counted.

Table 4.—Sample statistics for batch fecundity estimation of the central subpopulation of northern anchovy for various years. (See Addendum for 1985 data.)

Statistic	1951-60*	1978	1979	1980	1981	1982	1983	1984
$n^\dagger$	19	23	44	33	127	109	83	87
Linear regression coefficient (b)	532	279	693	563	752	617	588	532
Linear regression intercept (a)	1,122	2,023	−4,410	−1,891	−1,979	−180	−1,002	−554
$s_{y \cdot x}{}^\ddagger$	2,752	3,103	2,935	1,276	2,522	2,583	1,282	1,281
Sample mean batch fecundity ($\bar{Y}$)†	10,270	7,546	8,506	7,745	9,083	10,031	5,828	5,862
Sample mean ovary-free fish weight ($\bar{w}$)†	17.18	19.76	18.64	17.10	14.70	16.54	11.63	12.06
Sample standard deviation of fish weight (s_w)	6.57	6.62	5.32	4.77	5.81	4.41	4.75	5.54
$\Sigma(w-\bar{w})^2$	777	964	1,208	728	4,253	2,100	1,850	2,639
Mean fish weight from survey ($\bar{\bar{w}}$)	—	—	—	17.50	16.20¶ 13.40	18.60	12.90¶ 11.20 9.63	12.02
Standard error of fish weight ($s_{\bar{\bar{w}}}$)	—	—	—	0.96	0.47¶ 0.52	0.37	1.56¶ 0.79 0.37	0.46
Adjusted mean batch fecundity for ovary-free fish weight = 14.95 g§	8,900	4,597	6,241	6,423	9,237	9,055	7,870	7,640
Standard error of batch fecundity for 14.95 g fish §	536	494	358	408	207	225	264	256

*From MacGregor (1968).

†Sample mean batch fecundity ($\bar{y}$) and mean fish weight ($\bar{w}$) are computed from data set with n fish.

‡Standard deviation about the line.

§Computed from analysis of covariance.

¶Computed from individual cruises (1981 values for two cruises and 1983 for three cruises).

vilinear model; 2) its regression coefficients have a simple biological meaning (b = batch fecundity/gram female weight, $\bar{Y}$ = mean batch fecundity); and 3) for the egg production estimate, the fecundities of the largest and smallest fish are not as critical as for the fish in the middle range, which is well explained by the simple linear model.

Analysis of these eight data sets also indicated that the standard deviation of the batch fecundity is a linear function of the female weight (R^2 ranges from 0.2 to 0.6). The minimum variance and unbiased estimates of the regression coefficients can be obtained through a weighted least squares regression with the inverse of the variance as the weight (Draper and Smith 1981). In most cases the standard errors of regression coefficients from the weighted least squares were smaller than those from the regular least squares.

Table 5.—Mean square error (MSE)* of linear (unweighted and weighted) and nonlinear (exponential and power function) models for relationship between batch fecundity and fish weight of northern anchovy, based on data sets by years.

	Regression models				
	Linear		Nonlinear		
Year	Unweighted ($\times 10^{-6}$)	Weighted	Exponential ($\times 10^{-6}$)	Power function	Sample size (n)
1951-60	7.6	9.0	7.3	7.5	19
1978	9.6	8.3	10.2	8.1	23
1979	6.5	7.4	7.8	8.3	44
1980	1.6	1.5	1.5	1.5	33
1981	6.4	5.6	7.1	6.4	127
1982	6.8	4.9	6.7	6.6	109
1983	1.7	1.9	1.9	1.6	83
1984	2.2	1.3	3.5	2.3	87

*MSE = $\Sigma(\hat{Y}-\hat{Y})^2/(n-2)$ where $\hat{Y}$ is the estimated batch fecundity from subsamples. MSE, rather than R^2, is used to measure the fitness of the model because R^2 is inappropriate for nonlinear equations.

Precision of Batch Fecundity Estimation and the Numbers of Females

In the previous sections, we have considered the optimum number of ovarian tissue samples of northern anchovy relative to costs and have examined various regression models for biases in expressing the fecundity-fish weight relationship. This analysis indicated that if two or three tissue samples per fish are taken, further precision can be obtained only through increasing the numbers of fish in the sample, and we also showed that for anchovy the simple linear model is the preferred regression model. The objective of this section is to determine the effect of the number of females on the precision of the regression estimates of batch fecundity ($\hat{Y}$) using the linear model. All the historical data for batch fecundity in the northern anchovy (1951-84) were used in this analysis.

The average batch fecundity for the spawning population can be estimated ($\hat{Y}_{\bar{\bar{w}}}$) from a regression model where $\bar{\bar{w}}$ is an average of ovary-free female fish weight for the survey. Batch fecundity is based

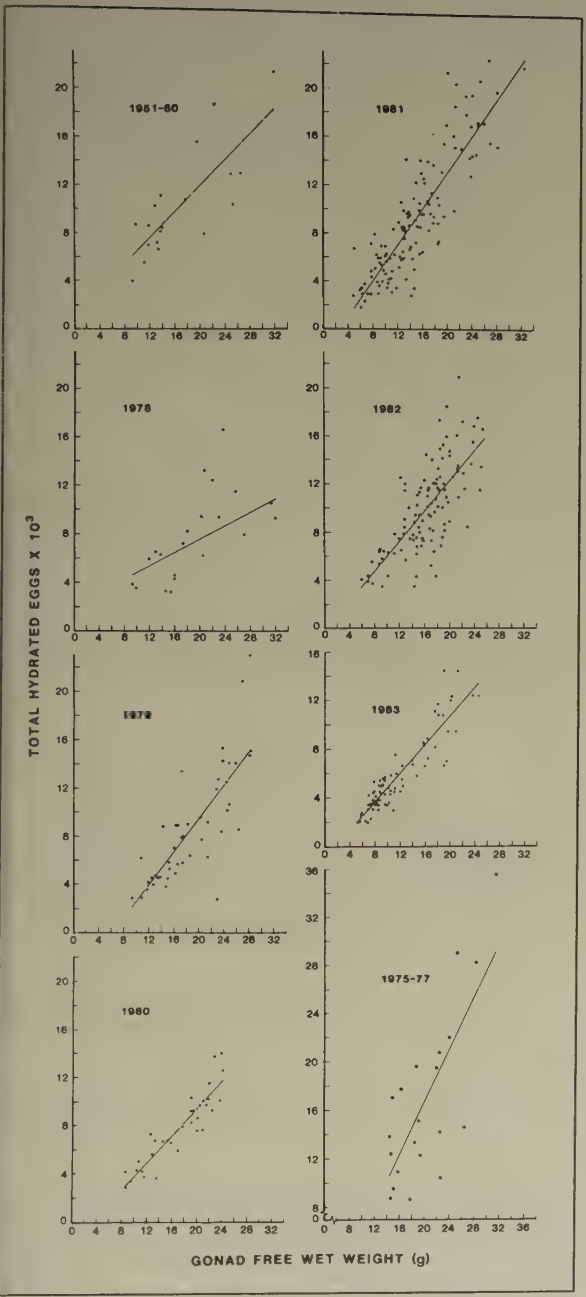

Figure 4.—Relation between batch fecundity of northern anchovy and their weight in formaldehyde solution (less ovary) for various years and subpopulations. All panels except lower right are for central subpopulation; lower right is for northern subpopulation, 1975-77, from Laroche and Richardson (1980). Fecundity estimates for the central population for 1951-60 are from MacGregor (1968) and are estimated using the oocyte frequency distribution method. Equations for lines are given in Table 4 for central subpopulation. For northern subpopulation $\tilde{Y} = -5287 + 1098\,w$, $R^2 = 0.55$ (our calculation from Laroche and Richardson 1980).

on ovary-free weight whereas the weight of each female in the survey includes the ovary weight. Thus the mean weight of females ($\hat{w}$) in the survey must be adjusted to ovary-free weight to estimate the batch fecundity for the average female in the population. This is done by multiplying female weight by 0.95, i.e., $\bar{\bar{w}} = 0.95 \cdot \hat{w}$ (Hunter and Macewicz 1980) (Table 4). The average female weight in the fecundity samples ($\bar{w}$) may be different from $\bar{\bar{w}}$ because the fish used in the fecundity estimate are a small subsample of the thousands of mature fish taken in a survey. Hence, $\bar{\bar{w}}$ is preferable for biomass estimation. Generally speaking, $\bar{w}$ and $\bar{\bar{w}}$ are similar although occasionally the difference has been as great as 2 g.

The precision of the regression estimate of batch fecundity is measured by its coefficient of variation, $cv(\tilde{Y}_w)$. The variance of $\tilde{Y}_{w^*}$ for a particular fish weight w^* is equal to

$$\sigma^2 \cdot \left[\frac{1}{n} + \frac{(w^* - \bar{w})^2}{\sum (w - \bar{w})^2} \right] \tag{10}$$

where σ^2 is the variance around the regression line (estimated by s_ξ^2) and w^* is measured without error. To evaluate the effect of numbers of fish on the precision of the regression estimate, we calculated the cv of $\tilde{Y}_{\bar{w}}$ and $\tilde{Y}_{\bar{w}-2}$ for each of the data sets. Four elements affecting the variance of $\tilde{Y}_{w*}$ are σ^2, n, w^*, and the sums of squares ($\Sigma(w-\bar{w})^2$). Although the variances of fish weight (s_w^2) are quite similar among years, the sum of squares ($\Sigma(w-\bar{w})^2 = (n-1)s_w^2$) are different (Table 4). A small value of $\sigma^2_{\tilde{Y}_{w^*}}$ results from either a large n and/or a wide range of fish weights. Increasing sample size n and/or increasing $\Sigma(w-\bar{w})^2$ reduces $\sigma^2_{\tilde{Y}_{w^*}}$.

The coefficient of variance of $\tilde{Y}_{\bar{\bar{w}}}$ was expressed as a function of the number of fish in the fecundity sample. For this analysis we used two versions of the power function ($cv(\tilde{Y}_w|n) = \alpha \cdot n^\beta$): One in which $\bar{\bar{w}}$ is assumed to be the same as $\bar{w}$ and the other in which $\bar{\bar{w}}$ is equal to $\bar{w} - 2$ [Equations (11) and (12)]. In the latter equation, the cv of $\tilde{Y}_{\bar{w}-2}$ sets the upper bound for the cv of $\tilde{Y}_{\bar{\bar{w}}}$.

$$cv\left(\tilde{Y}_{\bar{w}-2}\,|n\right) = 0.644\,n^{-0.735} \tag{11}$$

$$cv\left(\tilde{Y}_{\bar{w}}\,|n\right) = 0.438\,n^{-0.561} \tag{12}$$

For a sample size of 20 fish, the cv of $\tilde{Y}_{\bar{\bar{w}}}$ falls between 0.07 and 0.08, and for a sample size of 60 it ranges between 0.03 and 0.04 [depending upon whether Equation (11) or (12) was used] (Fig. 5). Assuming that the coefficient of variation for the fecundity estimation should be less than 0.10, one should select a sample size that yields a cv of $\tilde{Y}_{\bar{\bar{w}}} = 0.05$ because Equations (11) and (12) assume the fish weight (w) is measured without error; thus, for northern anchovy, a sample size of 50-60 females is adequate. In the biomass estimation, the cv for the fecundity estimation is a function of variances of both $\tilde{Y}_{\bar{\bar{w}}}$ and $\bar{\bar{w}}$. The variance formula for the fecundity estimate including variance of $\bar{\bar{w}}$ is given below.

$$\sigma^2_{\tilde{Y}_w} = \sigma^2_{\left[\bar{Y} + b(\bar{\bar{w}} - \bar{w})\right]} = \sigma^2 \left(\frac{1}{n} + \frac{(\bar{\bar{w}} - \bar{w})^2}{\sum (w - \bar{w})^2} \right) + b^2 \sigma^2_{\bar{\bar{w}}} \tag{13}$$

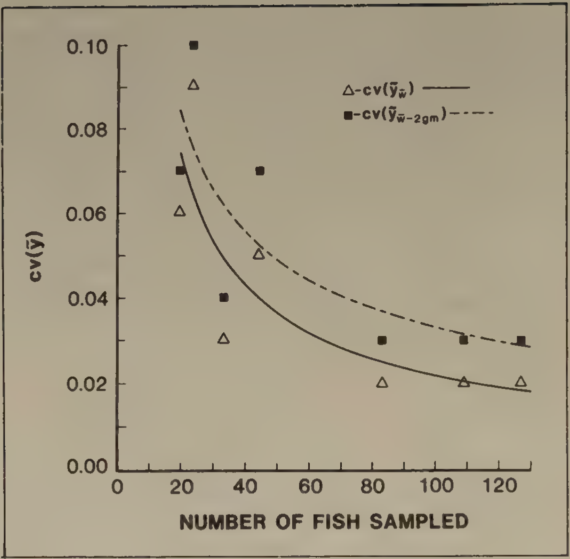

Figure 5.—Coefficient of variation (*cv*) of the regression estimates of batch fecundity for the average female anchovy weight as a function of the number of fish used to estimate fecundity in various years (see Table 4). Solid line is the *cv* for the average weight of females in the fecundity sample, and dashed line is the upper bound of the *cv* for the average female weight in the population.

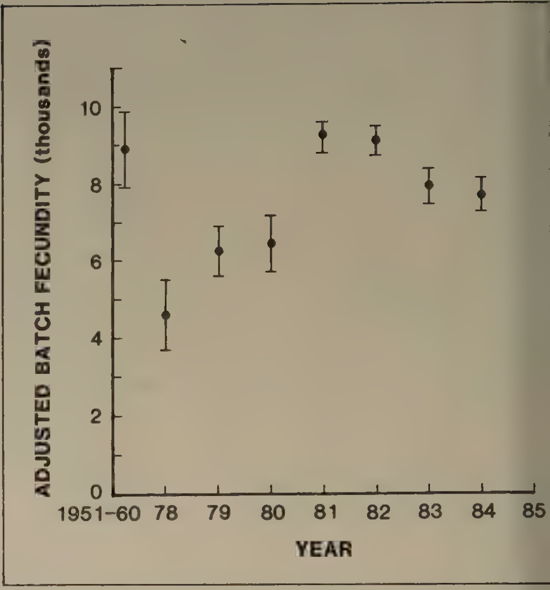

Figure 6.—Adjusted batch fecundity estimates for average female weight equa 14.95 g, and the 95% confidence interval (represented by vertical bars) by ye (see Table 4).

Variation of Batch Fecundity Among Years

The relation between batch fecundity and fish weight has been estimated annually for the egg production biomass estimation of northern anchovy because we believed that the relationship could change from year to year. Otherwise one equation would suffice for all years. To test this assumption, we performed an analysis of covariance to compare batch fecundity per female weight (regression coefficients, *b*) among years. The results show that not all slopes are the same, and have ranged from 279 eggs/g in 1978 to 752 eggs/g in 1981 (Table 4). Moreover, the average batch fecundity for a female of 14.95 g (the mean weight of all females in the fecundity samples when all samples are combined) also differs significantly among years (Fig. 6). The average number of eggs produced per spawning by a standard female of 14.95 g has varied by a factor of 2 over the last 7 yr (1978-84). This does not take into account the variation in average weight of females in the spawning population which also shows significant interannual variation. No doubt exists that batch fecundity of the northern anchovy population varies interannually and that it is necessary to estimate batch fecundity for each biomass estimation. On the other hand, if an average fecundity for all years (1951-84) is necessary, the following equation can be applied: $\hat{Y}_w = -1104 + 614\ w$.

SUMMARY

1. Laboratory methods are described for estimating the batch fecundity of fishes with indeterminate annual fecundity using counts of the number of hydrated eggs within weighed tissue samples of the ovary.

2. In northern anchovy, location of the tissue sample within ovary has no effect on counts of hydrated eggs. Location of tiss samples may be important in fishes with larger ovaries or possi in anchovy in the earliest stages of hydration. Thus, position effe must be evaluated for each species and sampling time.

3. The optimum number of tissue samples was 2 or 3 per ov in northern anchovy, but a higher number may be necessary if p tion effects exist.

4. To maintain the coefficient of variation for the average fecu ity of the population at less than 10% requires a sample of 50 more females.

5. In northern anchovy, a simple linear regression model preferable to nonlinear models for expressing the fecundity-fem weight relation but this must be evaluated for each populatio

6. For the egg production estimates, the average batch fecun of the population can be calculated from the average weight of females in the population (based on a weighted sample mean) us batch fecundity-female weight regression model.

7. The batch fecundity of northern anchovy has varied significa among years (1951-84) indicating the batch fecundity-fish weight tion must be estimated for each egg production estimate.

LITERATURE CITED

BAGENAL, T. G.
1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. John Wiley, N.Y.

BLAXTER, J. H. S., and J. R. HUNTER.
1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20:1-223.

CASSIE, R. M.
1954. Some uses of probability paper in the analysis of size frequency distribution. Aust. J. Mar. Freshwater Res. 5:513-522.

DeMARTINI, E. E., and R. K. FOUNTAIN.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547-560.

DRAPER, N. R., and H. SMITH.
1981. Applied regression analysis, 2d ed. John Wiley, N.Y., 709 p.

FULTON, T. W.
1898. On the growth and maturation of the ovarian eggs of the teleostean fishes. Annu. Rep. Fish. Board Scotl. 16:88-124.

HARDING, J. P.
1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

HICKLING, C. F., and E. RUTENBERG.
1936. The ovary as an indicator of the spawning period in fishes. J. Mar. Biol. Assoc. U.K. 21:311-317.

HISLOP, J. R. G.
1975. The breeding and growth of whiting, *Merlangius merlangus* in captivity. J. Cons. int. Explor. Mer 36:119-127.

HISLOP, J. R. G., A. P. ROBB, and J. A. GAULD.
1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish. Biol. 13:85-98.

HOLDEN, M. J., and D. F. S. RAITT.
1974. Manual of fisheries science. Part 2—Methods of resource investigation and their application. FAO Fish. Tech. Pap. 115 (Rev. 1), 214 p.

HUNTER, J. R.
1985. Preservation of northern anchovy in formaldehyde solution. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 63-65. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

HUNTER, J. R., and S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., and R. LEONG.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

HUNTER, J. R., and B. J. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 79-94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

JOSEPH, J.
1963. Fecundity of yellowfin tuna (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) from the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 7:255-292.

LAROCHE, J. L., and S. L. RICHARDSON.
1980. Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington. Fish. Bull., U.S. 78:603-618.

LeCLUS, F.
1977. A comparison of four methods used in fecundity determination of the pilchard, *Sardinops ocellata*. Fish. Bull., S. Afr. 9:11-15.
1979a. Dry mass yolked oocytes of the South West African pilchard *Sardinops ocellata* in relation to maturity stages and spawning cycles, 1972-1974. Investl. Rep. Sea Fish. Brch. S. Afr. 119, 29 p.
1979b. Fecundity and maturity of anchovy *Engraulis capensis* off South West Africa. Fish. Bull., S. Afr. 11:26-38.

MacGREGOR, J. S.
1957. Fecundity of the Pacific sardine (*Sardinops caerulea*). Fish. Bull., U.S. 57:427-449.
1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Fish Game 54:281-288.

SCHEFFÉ, H.
1959. The analysis of variance. John Wiley, N.Y., 477 p.

YAMAMOTO, K.
1956. Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. Fac. Sci. Hokkaido Univ., Ser. VI, Zool. 12.

ADDENDUM

Since this volume went to press an additional estimate of the biomass of the central subpopulation of northern anchovy was made in 1985. Batch fecundity parameters (listed in Table 4) for 1985 were as follows: n, 85; b, 682; a, $-2{,}036$; $s_{y \cdot x}$, 1,936; $\bar{Y}$, 8,490; $\bar{w}$, 15.43; s_w, 4.26; $(w-\bar{w})^2$, 1,524; $\bar{\bar{w}}$, 14.50; $s_{\bar{\bar{w}}}$, 0.32; adjusted mean batch fecundity for 14.95 g fish, 8,156; and standard error of batch fecundity for 14.95 g fish, 211.

Pacific Coast Groundfish Management: Evolution and Prospects

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SUMMARY

Although federal management of Pacific coast groundfish strongly resembles previous state and international management programs, the current fishery management plan (FMP) contains important new elements as well. The groundfish FMP adopts state fishing gear regulations, but seeks more coastwide uniformity. As in previous international agreements, foreign fishing is limited to Pacific whiting and jack mackerel (with minimum incidental catch of other groundfish), and is prohibited in areas sensitive to U.S. interests. Development of major domestic rockfish and joint venture fishing has changed the fishery and has challenged the management system to devise approaches to new problems.

Annual harvest quotas or "guidelines" were established for several commercial species. These are based on "optimum yield" estimates derived from biological stock assessments. A major advance in the FMP is its flexible procedure for modifying the annual harvest guidelines in response to new information and changing fishery conditions. Individual vessel trip catch and frequency limits, designed to extend the rockfish fishery over the year, represent another important innovation. These regulations affect not only the pace and volume of catch, but also the distribution of catch among size-classes of vessels. In addition, the individual vessel trip limit reduces the economic incentive for greater vessel catching capacity.

Further progress could be made in setting optimum yield objectives and in addressing economic objectives of management. The FMP's optimum yield discussion ignores ecological interactions among species, and it treats aggregate yield from a mix of rockfish species as the sum of the yields from individual stocks. This is because there are no quantitative ecological models. Research suggests that optimum yields

for individual species should not be independent of the quantity and mix of other species being fished. Further, even if each species is ecologically independent, in multi-species harvesting some species are fished at greater or lesser rates than they would be in a single species harvest. Development of multi-species optimum yields should be high on the research agenda.

To generate greater net economic benefits, access must be limited either with license limitation or with individual fisherman quotas. License limitation provides minimal control over the excess vessel investment. Licenses do not replace the various harvest quotas, however, since the multi-species fleet would still over-fish individual species.

To forestall excessive capital investment among licensees, some meaningful control over up-grading fishing technology and vessel replacement is needed. "Individual fisherman quotas" eliminate the need for these controls by designating the quantity of fish to be caught by each fisherman. Despite the possible additional administrative and enforcement costs of individual quotas, this approach should be seriously considered for Pacific coast groundfish.

INTRODUCTION

During four years development, the Pacific Fishery Management Council (PFMC) worked out an innovative and ambitious plan for Pacific coast groundfish. The final plan covers a broad variety of fish species taken by the whole gamut of fishing methods (trawls, pots, lines and gill nets). It addresses fish stocks in all stages of development and depletion. It establishes harvest guidelines for the more heavily exploited fish stocks, and includes a variety of regulatory methods to assure that these guidelines are met. Finally, and possibly most important, the groundfish fisheries management plan (FMP) provides flexible procedures for altering harvest guidelines and associated regulations in response to new information.

Both the FMP and the periodic reports compiled by the Groundfish Management Team (hereafter called "the team") provide comprehensive documentation of the fish harvests, fishing fleet, and management alternatives considered. Therefore, I provide only a brief background summary on the fishery and plan in this paper. Beyond that summary, I describe the underlying management policy and anticipate modifications that might be necessary to meet reasonable biological and economic objectives.

In reviewing and evaluating the management effort I focus on two particular aspects: setting "optimum yields" and the possible introduction of limited access to the groundfish fishery. These are two prevalent and controversial topics in fisheries management. Consideration of these demands intense scrutiny of basic assumptions and objectives and comprehensive analysis of economic and ecological systems. Further development of a coherent policy for Pacific coast groundfish management requires careful examination of these issues. My objective here is not to present detailed proposals for changing groundfish management. Rather, I will suggest some approaches for further consideration, and contribute to public discussion of these issues--a discussion that must precede any effective consensus in support of revised management strategies.

SCOPE OF THE GROUNDFISH PLAN

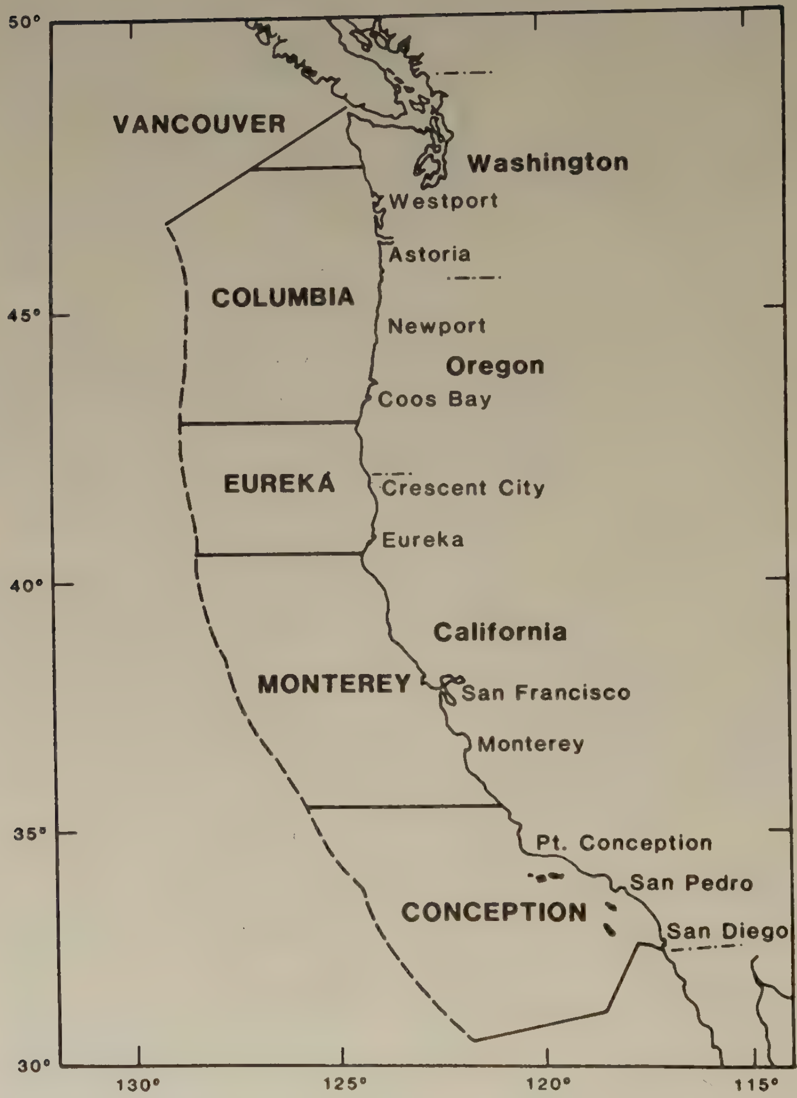
The groundfish FMP covers commercial and recreational fishing in the three to 200 mile zone of five International North Pacific Fisheries Commission (INPFC) statistical areas on the Pacific Coast (Figure 1). Only one significant area of the groundfish fishery -- Puget Sound-- is not covered by the plan. Total shoreside and joint venture harvests increased from 57,000 mt in 1976 to 187,000 mt min 1982, and then declined slightly to 170,000 mt in 1983 (Table 1). The recent decline was primarily due to the decreased catch of widow rockfish.

Gross ex-vessel value of shoreside landings grew rapidly from 1976 through 1982 caused both by rising prices and increasing catch. Nominal ex-vessel price-per-ton for domestic groundfish peaked at $532/mt in 1979, dropped about 23 percent from 1979 to 1980, and then climbed back almost to the 1979 level by 1983. After adjustment for inflation, however, the 1983 average ex-vessel price is 24 percent below the 1979 price, and lower than the average 1976 price. These changes in gross value of landings are caused both by fluctuations in the market for fish and by changing species composition in the catch. Higher-priced species, like sablefish and the soles, account for an decreasing proportion of the total harvest, while lower-priced species, like rockfish, account for an increasing share.

During the same time span, from 1976 to 1983, foreign catch off of Washington, Oregon and California fell from 225,000 mt to nothing. During 1984, both Polish and Soviet fishing fleets are gaining renewed access to the Pacific coast whiting fishery. Preliminary indications are that around 30,000 mt will be released for foreign fishing this year. Joint venture fishing, arranged primarily through one firm (Marine Resources Company) grew rapidly after 1978. Current projections indicate that the 1984 catch may reach 100,000 mt, for the first time exceeding shoreside landings.

Eighty-four species are currently listed in the groundfish management unit. For practical purposes these can be roughly divided into five categories: rockfish, Pacific whiting, sablefish, other roundfish, and flatfish. Table 2a presents the distribution of catch by species groups and among the INPFC statistical areas, while Table 2b displays the catch by gear type. Of the $70.4 million in 1982 ex-vessel revenue, 82 percent was earned by trawl vessels, 6.7 percent by fishermen using fish pots and traps, and the remainder by vessels using longline and other gears. About 15 percent of the dollar value of trawl vessel sales were from over-the-side deliveries for joint venture fishing companies operating foreign-owned processing ships.

Pacific whiting, which accounts for the largest harvested tonnage, is caught primarily by domestic fishing vessels in joint venture operations. Rockfish, the second leading species group, includes Pacific Ocean perch, shortbelly rockfish, widow rockfish and the so-called Sebastes complex. The Sebastes complex is dominated by yellowtail and canary rockfish in the INPFC Vancouver and Columbia areas and by chilipepper and boccacio rockfish in the Monterey and Conception areas. The principal species in the flatfish group are Dover sole, English sole and petrale sole. Sablefish, accounting for the fourth largest tonnage, is caught by a large number of fish pot fishermen as well as by trawl gear. Pacific cod and lingcod dominate the "other roundfish" category. Other miscellaneous fish in the FMP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California
Westport
Astoria
Newport
Coos Bay
Crescent City
Eureka
San Francisco
Monterey
Pt. Conception
San Pedro
San Diego

Figure 1. Pacific Coast groundfish management areas.

Table 1. 1975-1983 Pacific Coast groundfish harvest, quantity and ex-vessel value

Year	Domestic Harvests				Foreign[1]	
	Shoreside 1,000 mt	Shoreside $ mil.	Joint Venture 1,000 mt	Joint Venture $ mil.	1,000 mt	$ mil.
1976	57.0	19.4	-	-	255.0	unk.
1977	59.8	20.7	-	-	118.0	unk.
1978	71.6	34.5	0.9	0.1	98.0	13.3
1979	90.0	47.9	8.8	1.2	117.0	15.9
1980	87.9	37.1	26.8	3.3	44.6	5.5
1981	103.9	46.8	43.8	6.3	70.9	10.2
1982	119.0	60.0	67.7	10.4	7.3	1.1
1983	97.7	52.2	72.1	10.2	-	-

[1] Foreign fishery value calculated on assumption that price is equal to joint venture average price per metric ton.

Sources: 1976 data from Pacific Coast Groundfish FMP, p. 8-3.
1977-1980 data from C. Korson, Economic status of the Washington, Oregon, and California groundfish fishery in 1981. NMFS, Southwest Regional Office, Termnal Island, CA.

1981-1983 harvest quantities from PACFIN Report No. 002.

1981-1983 ex-vessel values from PACFIN Report No. 022.

Table 2a. 1982 Pacific Coast commercial groundfish harvests by INPFC area by species group (metric tons)

Species Group	Vancouver	Columbia	Eureka	Monterey	Conception
Rockfish	6693	27336	8170	14996	4466
Sablefish	2422	6348	3791	5083	946
Pacific whiting	30646	36410	8407	115	tr
Other roundfish	1361	1986	559	848	163
Flatfish	3860	14157	7411	6643	563
Others	107	109	99	143	111
Total	45089	86346	28437	27828	6222

Source: PACFIN Report No. 001. Includes joint venture catch.

Table 2b. 1982 Pacific Coast commercial groundfish harvests by gear type and species group (metric tons)

Species Group	Groundfish Trawls	Pots & Traps	Shrimp Trawl	Gill-Nets	Hook & Line
Rockfish	55646	30	1091	1639	3247
Sablefish	10159	6494	79	144	1657
Pacific whiting	75577	-	-	-	1
Other roundfish	4264	5	95	180	353
Flatfish	32419	1	128	45	11
Others	374	1	2	145	38
Total	178,439	6531	1395	2153	5307

Source: PACFIN Report No. 009.

are the various sharks, skates, rays, rattails, and jack mackerel taken north of 39° N. latitude.

The number of domestic fishing vessels active in the groundfish fishery changed rapidly from 1976 to 1983 (Table 3). Of particular significance is the trawler fleet, which increased by 174 vessels. Most of the new vessels entering the fleet were larger, more powerful vessels with improved navigation, high-speed winches, stern ramps and mid-water trawling capability. These vessels tend to focus on the high-output, but lower-unit-value fisheries such as widow rockfish and Pacific whiting. Some of these vessels also participated in joint venture catches. Because of the ex-vessel prices and very high costs of borrowing capital, many of these newer vessels encountered financial difficulties.

Table 3. Groundfish fleet size, 1976-1982

Year	Number of Vessels with Specified Gear:		
	Otter Trawl	Pot/Trap	Longline
1976	269	36	N/A
1977	286	60	N/A
1978	351	119	N/A
1979	472	207	N/A
1980	458	116	205
1981	409	66	191
1982	443	82	208

Sources: 1981 and 1982 Status Reports on the Pacific Coast groundfish fishery, compiled by C. Korson, NMFS, Southwest Regional Office; and PACFIN Report No. 022, PFMC Source Report: Commercial Groundfish Estimated Dollar Values of Landed Catch.

SYNOPSIS OF FMP CONTENT

The Pacific coast groundfish FMP provides a lengthy discussion of alternatives to and implementation procedures for those measures chosen by the Pacific Fishery Management Council. I find the following five elements to be the most essential features of the plan.

BIOLOGICAL YIELDS

For each important groundfish stock, the team established a level of "maximum sustainable yield" (MSY), defined as the "average over a reasonable length of time of the largest catch which can be taken

Table 4. Pacific Coast groundfish harvests, estimated maximum sustainable yields and allowable biological catch (ABC) (metric tons)

Species	Annual Harvest			Estimated	1984
	1976	1982	1983	MSY	ABC
Pacific Ocean perch	2,336	893	1,659	5,300	1,550
Widow rockfish	-	25,445	9,904	10,714	9,300
Shortbelly rockfish	-	3	1	44,250	10,000
"*Sebastes* complex"	20,051	35,515	35,919	33,000	28,000
Boccacio	unk	unk	unk	6,100	6,100
Canary	unk	4,296	3,654	5,900	2,700
Chilipepper	unk	unk	unk	2,300	2,300
Yellowtail	unk	8,715	8,887	5,000	3,200
Remaining rockfish	unk	unk	unk	unk	13,700
Sablefish	7,028	18,592	14,533	13,400	13,400
Pacific whiting					
Shoreside	trace	1,023	1,051		
"Joint Venture"	0	67,465	72,100	175,500	175,500
Foreign Catch	231,000	7,089	0		
Pacific cod	2,165	910	597	unk	3,100
Lingcod	2,542	3,809	4,146	7,000	7,000
Other roundfish	5,187	4,918	4,762	10,100	10,100
Dover sole	13,179	20,916	19,819	19,000	19,000
English sole	4,488	2,771	2,336	4,500	4,500
Petrale sole	2,816	2,619	2,193	3,200	3,200
Other flatfish	4,690	11,691	9,581	15,400	15,400
Totals	295,482	193,550	169,329	341,664	300,050

Sources: 1976 harvests from Groundfish FMP, Table 8. 1982 and 1983 harvests from PACFIN Report No. 002. MSY estimates from the FMP, Table 13 and various reports of the Groundfish Team. ABC's and OY's from the 1984 regulations (Federal Register, Vol. 49, No. 5; January 9, 1984 pp. 1060-1061).

Notes:
- "*Sebastes* complex" is all rockfish except Pacific Ocean perch, widow and shortbelly rockfish, and *Sebastolobus* sp.
- unk = unknown harvest level.

continuously from a stock" (FMP p.2-5). Due to variations in recruitment, ocean conditions and other uncontrolled factors, however, it may not be desirable to catch the MSY each year. Accordingly, the FMP defines "acceptable biological catch" (ABC) as the "seasonally determined catch that may differ from MSY for biological reasons". ABC may be lower then MSY for depleted stocks, like Pacific Ocean perch, and it may be higher than MSY for newly exploited stocks, like widow rockfish.

The FMP lists estimated MSY and ABC for sixteen principal species and species groups in each of the INPFC areas of the Pacific Coast groundfish fishery (Table 4). These estimates rely upon analyses ranging from detailed, long-term assessments to "first approximations". For Pacific whiting, for example, there are extensive studies by Soviet and U.S. scientists that support the estimated MSY of 175,000 mt. Ichthyoplankton and hydroacoustic/trawl survey information permitted the team to estimate the proportions of the total MSY occurring in each INPFC area. At the other extreme, only rudimentary stock assessments are available for lingcod, Pacific cod, "other flatfish", "remaining rockfish" or sablefish. Estimated ABCs are sometimes set as a proportion of recent annual harvest rates, where the proportion chosen is based upon collective judgement of the team as to the impact of recent harvest levels on the stock. Evidence used in this judgement includes anecdotal accounts from fishermen, estimated catch-per-efforts, changes in length or age composition in landings, and how long catch levels have been sustained.

OPTIMUM YIELD

For all but five groundfish species, "optimum yield" is defined as the amount taken with "legal gear". In other words, the optimum amount is the quantity harvested during a year by fishermen using gear that meets specifications in the plan. This approach to OY is applied to most of the rockfish species, all the flatfish, Pacific cod, lingcod and miscellaneous species. Gear restrictions are expected to protect juvenile fish and to maximize the yield-per-recruit for most of the species. Bag limits on recreational catch are three lingcod per day and 15 rockfish per day.

The FMP lists three main reasons for adopting the non-numerical OY approach. First, the fish stocks covered were not thought to be significantly depleted by commercial fishing at the time the FMP was developed. Second, this multi-species fishery naturally experiences simultaneous harvest of more than one target species and occasional large by-catches of non-target species. Grouping many species under a non-numerical OY "allows the flexibility to manage for maximum yield from the group as a whole rather than the maximum yield from each species". Third, management without using numerical quotas was expected to allow the existing fishery to continue with least impact on "fishermen's freedom".

A variety of special circumstances are cited by the groundfish plan as reasons to assign numerical OYs to some species. For Pacific whiting, widow rockfish, and shortbelly rockfish, the reason is that "they can be caught with mid-water trawls with minimal by-catches". Pacific Ocean perch is "severely depleted and requires special management consideration". For sablefish: "much of the catch is by directed effort with stationary gear", and "harvests in the Monterey Bay area deserve special attention". Optimum yields for these five in 1984 are equal to the ABCs listed in Table 4, except for sablefish. The sablefish OY is 17,400 mt, 30 percent greater than the ABC.

The PFMC selected a 20-year re-building schedule for Pacific Ocean perch, requiring a low catch level barely exceeding expected incidental catches. For widow rockfish the OY significantly exceeded the MSY during the 1982 and 1983. Presumably, the extent to which OY exceeds MSY determines the rate at which a virgin fish stock is fished down to MSY or some other desirable equilibrium level. As shown in Table 4, the 1984 ABC for widow rockfish is slightly below MSY. This reflects apparent biological over-fishing in some management areas.

BIOLOGICAL ASSESSMENT AND "POINTS OF CONCERN"

Because many of the stock assessments in the groundfish FMP were first-cut, preliminary estimates, and because the non-numerical OY procedure cannot completely protect all important fish stocks from over-fishing, the plan establishes a "groundfish management team" to continually monitor the status of each species and species group. This team is to look for "signs of biological stress", and to report to the council regarding appropriate management measures when a "point of concern" is reached. Specific conditions triggering the point of concern include: biomass falling below the level producing MSY, recruitment falling substantially below replacement level, fishing mortality exceeding that required to take the acceptable biological catch, catch for the year exceeding the acceptable biological catch, and other abnormalities occurring in the biological characteristics of the stock.

After considering the team's report and evaluating comments received during a subsequent public hearing, the council may recommend new management measures to the Northwest Regional Director of the National Marine Fisheries Service. If concurring, the Regional Director will publish proposed regulations, and allow adequate time for public comment before implementing the new regulations. This procedure permits significant flexibility in formulating regulations to achieve the biological conservation of fish stocks consistent with the optimum yields and allowable biological catches established by the council in the plan. Regulations can be changed without going through the full FMP amendment process.

FLEXIBILITY IN SETTING HARVEST GUIDELINES

The "Points of Concern" mechanism allows fast response to biological conservation problems, but does not allow for increases in OY or ABC. The FMP has other procedures, however, for in-season and between-season upward adjustments in OYs and ABCs. If the groundfish management team concludes that increasing catch of a species will not "stress" that or any other species, the team may recommend that the council increase OY or ABC. As with the point of concern, the FMP lists a series of criteria for triggering the upward adjustment in harvest guideline. These criteria include biological factors such as: low fishing mortality rate relative to MSY, large recruitment, large biomass relative to MSY, and any other pertinent factor.

Upward adjustments in numerical OYs are limited to 30 percent during any given year, while reductions under the points of concern procedure are not limited. Upward adjustments of more than 30 percent in a year must be implemented through a full FMP amendment process, which can taken 250 to 300 days. The council may recommend more than one upward adjustment in a year, so long as the sum of all increases does not exceed 30 percent of the original optimum yield. Acceptable biological yields may be changed by any amount. Consequently, the PFMC/NMFS regulations have much greater flexibility in regulating the harvest of non-numerical OY species.

REGULATIONS TO ACHIEVE OPTIMUM YIELD

The optimum yields and acceptable biological catch levels in the FMP represent the maximum recommended catches. A numerical OY is a legal quota, and the fishery regulations must assure that this level of catch is not exceeded during a given calendar year. Although ABC is not a legal quota, it may be taken as a "harvest guideline" for non-numerical OY species. The PMFC has formulated specific regulations to assure that catches do not exceed harvest guidelines for the Sebastes complex, a non-numerical OY species group.

As noted, most species are not assigned numerical OYs. Harvests of these species are regulated only by restrictions on legal gear, area closures, and recreational bag limits. "Legal gear" is defined by extensive and specific requirements regarding: the construction and mesh size in trawl net cod ends (specific to type of trawl operation and region), size and use of chafing gear, size of rollers or bobbins on groundfish trawls, locations for set nets (trammel and gill nets), and escape panels in fish traps. In addition, both traps and longlines must be attended at least once every seven days, and both must also be marked at the surface at each terminal end of the groundline with a pole and flag, light, radar reflector and a buoy displaying clear identification of the owner.

For species having numerical OYs, or for which there is a "point of concern", the "legal gear" requirements are supplemented by additional fishing regulations. The generic form of regulation is prohibiting additional landings once the OY or ABC is attained (for example, a fishing season closure). Because of the in-season flexibility built into the groundfish plan, however, the council may decide that increasing OY is more justifiable than closing the fishery. The FMP also seeks to prevent wasting fish by allowing minimal incidental catches occurring after the harvest guideline is reached. For example, fishing vessels are limited to a "trip limit" of 5,000 lb of sablefish whenever 95 percent of the OY is reached in a management area. The 1982 trip limit for Pacific Ocean perch, which is managed as a strictly incidental catch, was 10,000 lb or 10 percent of the total fish landed.

In 1979, well before the FMP was officially implemented, the domestic trawl catches exceeded established ABCs for Pacific Ocean perch and Dover sole in the Vancouver area, Pacific Ocean perch, canary rockfish, yellowtail rockfish and Dover sole in the Columbia area, and sablefish coastwide. Also, widow rockfish catches substantially exceeded the original ABC estimate in 1981. Warnings of "biological stress" provoked varied responses from the PFMC/NMFS management authorities.

No additional regulations were developed to manage the flatfish species even though the Dover sole harvest continued to slightly exceed the coastwide ABC in 1982 and 1983. The "legal gear" measures protected small flatfish, and the amount by which catch exceeded ABC was trivial in view of the low precision of the biological assessment. This presumably justifies the council's lack of action on flatfish.

When sablefish catch was projected to substantially exceed the team's initial OY estimate in 1982, the council imposed a trip limit of 3,000 lb for the last three months of the year. The OY was raised from 13,400 mt to 17,400 mt (by 30 percent). The 1982 catch total was even greater than this new OY. The sablefish regulations were augmented in 1983 by a 22 in. minimum size limit in all areas north of Point Conception (excluding Monterey Bay). The incidental catch allowance for undersize fish has varied, but is currently 5,000 lb per fishing trip. The council's intention is to close the fishery after the OY is reached. But the market for sablefish in 1984 seems to have declined to the point that the fishery is unlikely to take the ABC.

The council has modified regulations on Pacific Ocean perch harvests to keep that stock on its 20-year rebuilding schedule. In some INPFC areas the annual catch was projected to exceed the area's ABC. In November, 1983 the Columbia area was closed to Pacific Ocean perch fishing, but the 5,000 lb or 10 percent by weight trip limit was retained in other areas. The 1983 harvest reached 1,659 mt, 7 percent greater than the coastwide ABC. In July 1984 the council further recommended that the Pacific Ocean perch trip limit be changed to 5,000 lb or 20 percent by weight, whichever is less. This last variant of the incidental trip limit regulation was designed to prevent smaller trawl vessels from making daily fishing trips specifically targeting on the 5,000 lb of perch.

Much recent council management activity has involved widow rockfish and the Sebastes complex. Harvest guidelines for these are implemented mainly through trip catch limits, trip frequency limits, incidental catch allowances, and season closures. Following the groundfish management team's recommendations, Sebastes complex ABCs are established in two geographic areas separated by 43° N. latitude (later changed to 42° 50'). The area north of this line roughly corresponds to the Vancouver and Columbia INPFC areas, while the southern range includes Eureka, Monterey and Conception. In each area the trip limits are calculated to allow the fleet to fish all year, assuming usual seasonal patterns of fishing, without exceeding the OY. If the OY is reached, then the fishery is closed.

Annual widow rockfish harvests grew from 4,293 mt in 1979 to almost 28,000 mt in 1981, dropped to about 25,000 mt in 1982, and fell to 9,900 mt in 1983. During 1980-1982 the PFMC temporarily permitted the OY to substantially exceed the estimated MSY of about 11,000 mt. The widow rockfish fishery was exploiting a virgin biomass of relatively old fish. The temporarily high annual fishing rates were expected to reduce the standing biomass, presumably to levels that might sustain a near-MSY harvest.

Maximum use of the FMP provisions for in-season flexibility is evident in the history of rockfish regulations. A coastwide trip limit of 75,000 lb, was imposed on widow rockfish from mid-October, 1982 through February of 1983. The trip limit was reduced to 30,000 lb in

March of 1983 and further reduced to 1,000 lb in September. In 1984, the widow rockfish trip limit started out at 50,000 lb, but was reduced to 40,000 lb in May. Trip frequency for widow rockfish was limited to one per week beginning in January, 1984. Each of these regulatory actions was preceded by reports and recommendations from the groundfish management team, industry advisors and scientific and statistical committee.

The fisheries for other rockfish species developed close on the heels of that for widow rockfish. A 40,000 lb trip limit for the Sebastes complex with maximum frequency of one per week was established in the Vancouver/Columbia area starting in March of 1983. In mid-September the trip limit for the Vancouver/Columbia area was reduced to 3,000 lb, while a limit of 40,000 lb per trip with no maximum frequency was specified for south of 43° N. The trip limit in the northern area was reduced to 15,000 lb once per week, or 30,000 lb once per two weeks (at the option of the vessel operator) in May of 1984. Although none of these trip limits could be expected to precisely attain the OY over an entire year, they do represent an innovative attempt to simultaneously satisfy both the OY and year-around fishery objectives.

EVOLUTION OF MANAGEMENT REGULATIONS UNDER THE FMP

Commercial fishing regulations evolved fairly rapidly during the first two years of the plan's operation, largely because stock assessments found increasing evidence of over-exploitation as the fishery expanded. An additional impetus for regulatory change was the PFMC's decision to extend fishing seasons over as much of the year as possible. The objective of this is to avoid disrupting the flow of fresh groundfish fillets in domestic markets supplied by the Pacific Coast fishery. To do this and keep the annual catch within harvest guidelines requires that the rate, not just the annual amount, of catch be regulated. Individual vessel trip limits and trip frequency limits were selected as the mechanism for retarding the harvest rate. This is a significant and important change from the traditional "fishing season" regulation wherein participating fishermen are unrestricted regarding catch on individual fishing trips.

Catch and frequency limits on fishing trips have two main effects: they re-allocate economic returns among the various size-classes of vessels, and they improve opportunities for private firms to reduce costs of fishing. When trip limits are low enough to lengthen the fishing season, smaller vessels should take a larger share of the annual catch than they would otherwise, and their profitability should improve relative to that of new, larger vessels. Recognizing the higher minimum per-trip harvest requirements of large trawlers, the groundfish regulations allow fishermen to catch twice the per-trip limit of Sebastes, if they make such trips fortnightly rather than weekly. This somewhat lessens the re-allocation effect. But it cannot compensate larger vessels entirely, since the higher fixed costs of owning and operating a large vessel need to be spread over a greater annual revenue. In sum, the new, more powerful vessels are designed to take advantage of profit opportunities related to large harvest volumes that the trip catch and frequency limits preclude. To maintain year-around fishing and greater trip limits, the number of fishing vessels must be reduced.

A trip limit approach also causes a qualitative change in the traditional form of competition for fish. With free access to the "common property" fish stock, a vessel's ability to harvest more rapidly usually translates into a larger share of the total harvest. With both catch per trip and trip frequency limited, increased fishing vessel capacity is no longer rewarded immediately with a larger share of the catch. Under trip limits, a vessel's expected annual harvest depends upon the annual harvest guideline and the number of participating vessels. This assumes, of course, that the trip limit is smaller than the typical catch-per-trip taken before the limit was imposed. When the council first established a widow rockfish trip limit in 1982, the level chosen (75,000 lb) was not a significant constraint, even on larger vessels.

The 1984 widow rockfish management regulations include an aggregate catch quota of 9,300 mt, a trip limit of 40,000 lb (18.14 mt), and a trip frequency of one per week. Subtracting 100 mt reserved for incidental catch after the widow rockfish season closure, these regulations create 507 weekly vessel quotas. If there are 70 vessels participating in the fishery, they can fish a average 7.25 weeks each on widow rockfish, and each vessel has the opportunity to harvest about 133 mt of fish. This 133 mt is not specifically assigned to individual vessels. So there is still competition among vessels; but the competition will be different from before. A given vessel operator can take 18.14 mt as fast as possible each week, or he can fish at a slower (and possibly less costly) pace, or he can intersperse widow rockfish fishing with other forms of fishing during a given week. Overall, I would expect the widow rockfish harvest to generate a greater net economic return than before, due to somewhat lower fishing costs. Also, the rockfish fillets may bring a greater net return because they are produced at a more even pace, over a longer season.

Similar qualitative change in competition among commercial fishermen may be encouraged by the Sebastes complex trip limit and trip frequency regulations, and to a lesser extent the Pacific Ocean perch and sablefish incidental catch trip limits. The potential increased economic value from these trip limits is small, and this does not represent a shift toward economic efficiency objectives in groundfish management. It does represent a perceptible movement away from annual harvest quotas that encourage irrational and costly harvest methods.

OPTIMUM YIELD CONSIDERATIONS

As I noted in the introduction, further development of coherent groundfish management requires that optimum yield receive attention. Two aspects need to be discussed: the nature and function of optimum yield in the management regime, and the criteria for setting OY in a multi-species fishery. I will provide some insight into these issues, indicating why I think they are important and how the existing management framework deals with them.

NATURE AND FUNCTION OF "OPTIMUM YIELD"

The Magnuson Fishery Conservation and Management Act (FMCA) followed the International Law of the Sea in designating optimum yield as a central management objective. Since much has already been written about the optimum yield concept, it is unnecessary to belabor that discussion here. The American Fisheries Society Symposium on Optimum

Sustainable Yield (Roedel 1975) and the NMFS-sponsored National Workshop on the Concept of Optimum Yield (Orbach 1977) provide extensive guidance. Optimum yield, as a management objective, is largely an elaboration of the more narrowly defined concept of maximum sustainable yield. It is supposed to encompass economic, ecological and social factors, but development of practical techniques for determining OY in specific instances has been slow. As lamented by P.A. Larkin (1977), even a concerted attempt to explain optimum yield tends to become an "eclectic mishmash that was all things to all people".

To avoid this "mishmash", a specific and explicit presentation is needed. Since economic factors have been most extensively considered in commercial fisheries, the prospects seem brightest for introduction of economics into optimum yield. Quantitative economic models for fishery management are available, many developed specifically for fishery management plans (for example Anderson 1981). Given proper information regarding market prices, fishing costs, and a biological yield model, standard analytical methods are used to determine maximum sustained level of economic yield.

Economic efficiency, in its broadest sense, is the focus of this approach. In principle, economic efficiency requires a proper balance of greater fish production and greater production of a variety of other things that could be produced instead of fish. In the words of James Crutchfield (1977), "optimal utilization of fishery resources, like optimal utilization of any other natural resource, cannot be divorced from optimal utilization of all inputs--natural resources, capital, labor, and technological knowledge--in meeting the multitude of competing demands for all goods and services".

The groundfish FMP does incorporate some economic factors in setting OYs, but it does so clumsily and inexplicitly. With its great reliance on MSYs and ABCs as optimum yields, the Pacific coast groundfish FMP appears to seek maximized physical yield. But the management record belies this simple interpretation. No remedial action was taken by the council or NMFS when shortbelly rockfish and Pacific whiting harvests fell far short of the stated optimum yield. These shortfalls were not alarming, in my interpretation, because the nominal OYs are not intended to represent optimal catch levels. Both the PFMC and the industry advisors implicitly understand that optimum yield of shortbelly rockfish is far less than the stated 10,000 mt, and that the OY for Pacific whiting was substantially below the nominal 175,000 mt.

These numerical OYs are better understood as maximum, biologically safe levels of fish harvest. From an economic standpoint, harvest levels are desirable only if the price equals or exceeds the fishing cost: if there is a "market" for the fish. Since the domestic fishery could not profitably exploit these fish stocks, the real optimum is some undefined amount less than the stated OY. The substitution of "biologically safe" for "optimum", however, confuses the concept of an optimum catch level with the process of regulation. The maximum safe level may logically function as an upper limit, or harvest quota. Whether quotas and optimum yields need be the same is debatable.

Without involving economic and other factors in setting optimum yields, moreover, "biological factors" are often stretched and twisted to accommodate all kinds of management concern. Caution in the face of resource uncertainty, avoiding foreign fishing allocations, and political division of the catch among competing groups are some of the management motives hidden under the guise of "biological" conservation. To those who understand the role of biological research and stock assessment, the management process appears to be ad hoc. One rationalization is that "optimum yield is whatever the council decides it is". This may be procedurally correct, but it fails to meet the need for well-informed, understandable management criteria.

For non-sustained harvest levels, development of an economic rationale for optimum yield is even more essential. The FMP's discussion of widow rockfish and Pacific Ocean perch management provides no convincing biological reasons for choosing particular rates of growth or decline in the underlying fish stocks. Yet the rate of stock reduction, or "dis-investment", was chosen when widow rockfish OYs were set during 1980-1982. Similarly, the 20-year rebuilding schedule for Pacific Ocean perch implies an investment rate that pays off in future economic returns. If explicit criteria for these non-equilibrium harvest strategies were developed, management policy would be more transparent to reviewers, and the council less subject to misunderstanding and criticism (see Gunderson 1983).

MULTI-SPECIES ASPECTS OF OPTIMUM YIELD

Since ecological interactions are important in determining sustainable yields from a species complex, fishery managers have long struggled with the need for acceptable criteria in managing multi-species assemblages. Whole workshops have been devoted to investigating multi-species approaches to fisheries management (Mercer 1982; Hobson and Lenarz 1977). Prominent fisheries scientists warn against the errors caused by artificially compartmentalizing the fishery by managing individual species (Silvert and Dickie 1982). Collecting and analyzing appropriate data to make practical use of eco-systems models, however, has proved too difficult for most fishery research efforts. The groundfish FMP does not explicitly consider the ecological interactions among species. It seems to assume that each species stock is biologically independent. This is implicit in establishing ABCs for each species in each management area.

For various species that are linked by technological and economic factors, however, the FMP does make provisions for multi-species harvesting. The groundfish plan introduces the notion of species "targeting". A species is a "target" if it can be caught predominantly in pure loads. A trawl net, for example, will usually encounter more than one groundfish species in a given area, depth or mode of operation. By appropriate manipulation of the time of day, area, speed, depth and other operational factors, however, a fishing vessel skipper can often "target" on one or two species.

Disagreement undoubtedly exists as to when, and under what conditions fishermen can accurately target on some species. But, as a general rule, the mid-water schooling species, such as widow or shortbelly rockfish and Pacific whiting, can be caught in nearly pure tows. Similarly, the Sebastes complex can usually be caught without serious incidental catch of other species; but there is less agreement on the extent to which trawl vessels can target a particular species in the complex. In contrast, important members of the flatfish group tend to be caught in mixes with several commercial species (Adams and Lenarz, unpublished manuscript). This technological interdependence is addressed in the FMP by lumping some species into groups. Species that can apparently be "targeted" are given separate optimum yields.

As a provisional approach to multi-species optimum yield, this raises some further questions. First, how can the optimum yield for a species group, like the Sebastes complex, be derived from the "acceptable biological catches" of the constituent species? If there are ecological interactions among the species, or if the different species stocks are optimally exploited at different fishing rates, this may be quite difficult. Second, what is the best way to prevent the wastage of incidentally-caught fish of a prohibited species, or of a species whose quota has already been filled? Assuming that targeting is imperfect, some incidental catch of a numerical OY species may be taken while fishing for other species.

To date, the harvest guidelines from grouped species are constructed from the sum of ABCs for the species. This is a questionable practice. If two species are harvested simultaneously (the same fishing effort applies to both stocks), the optimum level of aggregate catch (or effort) for the mixed harvest would equal the sum of the individual species optima only by extraordinary coincidence. Only if exactly the same level of fishing effort achieves the optimum yield for each species would there be a simultaneous optimum. In any other case, the optimum multi-species harvest must be less than the summed optima for the individual species, considered separately. Full use of more abundant species would likely require that less abundant and less productive species stocks be fished to less than the MSY level. Thus grouping several species to establish harvest guidelines requires adoption of a "second best" approach that cannot achieve the maximum total yield from the group. By this reasoning, the optimum yield for the Sebastes complex must be lower than the sum of the MSYs for yellowtail, canary, boccacio, chilipepper and other rockfish. The groundfish FMP recognizes this fact, but does nothing about it.

Another problem for multi-species fisheries is that of incidental catch regulations. Species with individual quotas cannot always be caught in pure loads. Consequently, some widow rockfish or Sebastes complex species, for example, will be caught by vessels targeting other fish. This inadvertent incidental catch will occur even after a quota is reached and target fishing stops. Mortality due to handling the fish is very high, so discarded fish are generally not returned to the stock for later harvest, but are wasted. The manager's dilemma is how to enforce a harvest quota, and prevent the wastage of discards, while not unduly burdening the fishermen with gear and other restrictions on efficient harvest practices.

In their examination of alternative incidental catch controls, Marasco and Terry (1982) adopt an approach that minimizes the economic cost of incidental catch. The direct "cost" of discards is approximately measured by the ex-vessel value of discarded catch. Regulations to prevent incidental catch, however, involve two other costs: those incurred by management authorities in surveillance and enforcement, and costs borne by fishermen if they are forced to fish in less productive fishing areas or times, or with gear that provides lower gross earnings. It is not necessarily desirable to eliminate incidental catch, even though this would minimize the direct cost of discards, because the administrative costs incurred by management authorities and fishermen might exceed the value of the fish saved.

Minimizing costs in incidental catch regulation would be part of a coherent multi-species harvest policy with two main affects. First, incidental catch would be considered in setting OYs and size limits of fully-used fish stocks. If the cost of avoiding small sablefish in the Dover sole fishery exceeds the value of sablefish saved, for instance, the incidental catch limit on small sablefish should be raised. Second, this would affect the design of an operational quota system. When a known percentage incidental catch is not worth avoiding, that catch can be subtracted from the directed fishery quota and reserved specifically for incidental catch.

Current groundfish management regulations seem to have adopted an approach quite close to this for Sebastes and sablefish, and I would not focus on this as a major problem. It may become a problem however, if the domestic fisheries for Pacific whiting and shortbelly rockfish develop to their potential. When low rates of incidental catch are applied to very large harvest volumes, the incidental catch of some depleted species, like Pacific Ocean perch, may equal or exceed the designated harvest guideline. Managers need to be prepared to decide when to relinquish particular objectives relating to species, like Pacific Ocean perch. Although this species is high-priced and has great prominence in the history of the fishery, a time may come when the costs of avoiding incidental catch and waste of discarded fish exceed the economic value of the fishery for that species. It might be useful to have some agreed criteria for deciding when and if a species should be re-assigned to a multi-species aggregate or non-numerical OY group.

LIMITED ACCESS PROSPECTS

Limiting access to commercial fisheries has become increasingly acceptable to managers and industry. A variety of industry and scientific groups have urged the Pacific council to consider limited access in the groundfish fishery. Over the past two decades this interest has been attributable to several motives: increased economic efficiency in the commercial fisheries, increased income for successful vessels, easing pressures on management caused by over-built fleets, and in some cases improved conservation of stocks. Current high interest in groundfish limited access can also be attributed to the increased experience in the Canadian, Australian, Alaskan and Pacific coast fisheries, as well as the poor financial performance of many recently-built trawl vessels.

Adopting such a significant change in the groundfish regulatory approach would require long and careful deliberation of limited access concepts and options. The generic options are thoroughly reviewed in the recent reports of Meyer (1983), Pearse (1982), Sturgess and Meany (1982), Stokes (1979), and Rettig and Ginter (1978). While I do not intend to make any specific proposals in this paper, I think it is useful to review the principles involved and to consider how limited access might apply to Pacific coast groundfish.

RATIONALE FOR LIMITED ACCESS

The general case for limiting fishery access builds upon the well-known deficiencies of open competition for "common property" fish stocks. Without regulations, competitive commercial fishing fleets tend to economically and biologically over-fish. The principal reason for stock depletion with open access competition is that individual fishermen cannot control aggregate harvest rates. When many firms catch fish in competition with others, no individual act of conservation is likely to pay-off for that individual. With common property fish stocks, economic rationality on the part of individual fishermen does not favor fish stock conservation. This lack of opportunity to invest in fish stocks, not lack of knowledge and inclination, explains the lack of private conservation action.

To determine appropriate yields for important commercial fish stocks, fishery scientists devise quantitative concepts expressing the biological potential, such as MSY. Applying annual catch quotas to the open-access fishery may adequately insure biological conservation. But the basic economic incentives of the individual fishermen are largely unchanged. Instead of competing for dwindling stocks, the open competition is for a conserved stock. Individual incentive for conservation action remains weak, and economic rewards go to those fishermen who find ways to increase their individual catches, so long as their increased fishing costs do not exceed increased ex-vessel revenues. As ex-vessel prices rise, increased potential fishing profits attract additional investments in fishing capacity by both new and continuing participants.

Obviously, the degree to which the over-built fishing fleet becomes a real concern depends upon the potential net difference between costs and revenues. Pacific salmon provides the extreme example of very high ex-vessel prices teamed with potentially miniscule harvest costs. To prevent rapid stock depletion management strategy has forced the harvesters into technically inefficient operations. Even with severe restrictions on catch, fishing seasons, and harvest technology salmon fleets tend to be unreasonably large. Consequently, it is not surprising that limited entry was introduced first, and has been used most extensively, in salmon fisheries on the Pacific Coast.

Like the harvest quota, however, limiting the number of participants in a competitive fishery does not change the economic incentives of individual fisherman. Although the number of competitors is limited, fishermen still find it profitable to increase fishing capacity as long as the cost of such increase falls below the potential increase in revenue. Soon after the salmon limited entry program was introduced in British Columbia, managers had to impose various sorts of capacity limits on fishing operations. Economic studies showed that increased investment in capacity of the limited fleet was a substantial threat to economic returns from the fishery (Fraser 1979; Pearse and Wilen 1979).

Similarly, license limitation programs in Australian fisheries have been forced to include stringent fishing vessel capacity controls. In the northern prawn fishery, for example, fishing licenses can be transferred and even consolidated, so long as the new vessel has no more capacity than previous license holder's (Colin Grant, personal communication). To maintain a significant level of "economic rent", the regulators may have to continually anticipate and forestall technical innovations that, while increasing an individual's harvest capacity, simply raise the total cost of taking a fixed harvest. The economic evaluation of license limitation systems is not complete, but the debate has now turned to whether any substantial economic benefit will accrue from the program in the long run. Simply limiting the number of licensed fishermen does not assure improved economic performance of fisheries.

In recent years, economists have focused on forms of limited access that more directly address the underlying common property problem. The key is to establish a set of institutions that lessen individual incentives to compete for increased catch through expanded fishing capacity. "Racing for fish" needs to be replaced by incentives for low-cost production of available yield. There are two basic alternatives. First, quantitative rights to harvest fish (also called "individual fisherman quotas") could be established to allocate optimum yield. These rights can mimic conventional property rights established for other natural resources. Second, landings fees or royalties could be set to discourage excessive fishing capacity and effort. In a Canadian fisheries context, Pearse (1982) is a well known proponent of individual fisherman quotas; and Stokes (1983) developed this approach during discussions of north Pacific halibut license limitation.

The main advantage of the individual fisherman's quota is that it eliminates the basic economic incentive leading to overcapitalization of the fishing fleet. With a known, quantitative share of the allowable harvest, a commercial fisherman will no longer be strongly encouraged by the profit incentive to competitively increase his fishing power. Instead, the fisherman is encouraged to adopt fishing vessels and fishing methods that permit taking the licensed catch at the lowest cost. The individual fisherman's profit incentive is made consistent with overall cost minimization. Further, permitting transfer of quantitative rights in private market transactions would encourage broader economic efficiency by facilitating the redistribution of harvest rights to those fishermen most able and/or willing to harvest at low cost. Market prices of individual quota certificates would be expected to reflect the potential profits from fishing. Like prices for other natural resource commodities, the price for a harvest quota would represent a cost of doing business to the purchaser and a source of income to the seller.

Royalties on fish harvests could be an alternative to quantitative harvest rights, or they could be used in conjunction with quantitative rights as suggested by Pearse (1982; p. 94-95). As a direct cost of fishing the royalty would discourage excessive investment in fishing power. If the royalty rate is roughly equivalent to the hypothetical market price for a quantitative harvest right, the same incentive for cost minimization would occur under the two alternative approaches.

Two primary elements distinguish royalties from quantitative rights. First, government administrators, rather than private markets, would set the value paid per unit harvested. Second, with royalties the net economic value of harvesting fish would accrue to the public treasury rather than appearing as net income earned by private fishing businesses. To establish royalty rates with correct cost minimizing incentives, public administrators will have to collect and evaluate cost and revenue data from fishing operations. Interpretation of such data can be technically difficult because of the variety of crew share arrangements, non-cash transactions, bonus payments, and variability in harvest rates among vessels and over time. Fishermen opposed to a royalty system would not be inclined to provide the more accurate information.

To avoid this estimation problem, management agencies might dispose of quantitative fishing rights in a public auction. Again, this substitutes the competitive market for administrative computation. This is the way the U.S. Forest Service and the U.S. Minerals Management Service dispose of timber harvesting and mining rights on public land. But there are essential differences between these rights and any prospective fish harvesting rights. Mineral and timber sales confer exclusive rights to sever the minerals or timber from the land, while any prospective fishing rights would retain certain characteristics of the "commons". A right to harvest, say 10,000 mt of Pacific whiting, could be established as a salable right, but the harvest of fish is still from a common pool.

Another practical problem with royalties is that they are distinctly political. Like taxes, they are established and modified through legislative action. Royalties would not be viewed as a permanent feature of the fishery, but as a point for continual negotiation, lobbying, and tinkering.

In contrast, once quantitative rights are established, the competition for fish that now fuels political tinkering would no longer be a continual source of instability. Competition for fish among gear types, regions, and cultural groups would no longer fuel political debate and be a constant source of instability for the fishery. Through time and custom, such rights might assume the legitimacy of private property. As noted by Anthony Scott (1984) the community would then be expected to uphold the validity of fishing rights, help protect them from trespass, and support their exchange and subdivision by standard property right mechanisms.

Further, once the rights are established, their holders will have an interest in the long-term health of the fishery. They will be more willing to make the short-term sacrifices often required to conserve fishery resources. Therefore, the beneficial affects of establishing property rights and the corresponding conservation responsibilities are most evident with the individual harvest rights approach.

PROSPECTS FOR APPLICATION TO THE GROUNDFISH FISHERY

License limitation tends to follow conventional fishery regulation, focusing on fish stocks rather than fishing fleets (Stokes 1979). Licensing programs for Pacific coast salmon, herring and abalone, and for Australian prawns and rock lobsters exhibit this characteristic. If fishing capacity is specific to a species, a stock, or a coherent group of stocks, the "fishery" may be identified by a fish stock or stocks for management purposes. In this case, one can determine how the number of licenses issued is likely to effect fishing capacity, economic yield, and estimated optimum fleet size. When several distinct gear groups and many varieties of multi-purpose fishing vessels are involved, as in Pacific coast groundfish, it is not so simple.

First there is the problem of usefully defining the groundfish fleet. The fleet currently includes many part-time vessels that are used for a number of fisheries. They shift at seasonal or longer intervals among shrimp, rockfish, bottom-trawling, and joint venture fishing. If the crab catch rate is high, some vessels shift from groundfish into Dungeness crab for the winter season. Also, salmon trollers and crab pot fishermen can catch groundfish incidentally. The line between included and excluded vessels, required for licensing, must be carefully drawn. If the definition is too all-inclusive, neither the fleet nor capacity is limited. To limit capacity and still allow great variety in commercial fishing strategies, separate licenses could be issued for distinctive segments of the fishery. Southern California gill nets, Monterey Bay fish traps, sablefish/halibut longliners, mid-water trawlers, and shrimp/bottomfish trawlers are some likely categories. Each category has a characteristic locale, harvests a characteristic mix of species, and uses a distinctive gear. But there will necessarily be a significant overlap in species and stocks exploited by license categories.

Beyond the problem of fleet definition, a license limitation approach is not particularly well-adapted to the flexibility normally exercised in multi-purpose fishing operations. As noted in Huppert (1979), the ability to shift among substitute fishing modes may be essential to the long-run economic survival of these kinds of vessels. Trawlers move between shrimp and groundfish as the fish stocks and market conditions affect revenue-per-day-fished. To license a vessel just for shrimp, or to deny groundfish licenses to vessels that have recently fished only shrimp, could be disastrous to those vessels and economically inefficient. Flexibility in license transfer, division and consolidation among vessels might address this need for shifting among fishing activities. Whether or not this could be accomplished without a cumbersome and costly administrative apparatus remains to be seen.

The other side of this coin is that limiting licenses to fish cannot effectively control the amount of fishing for any given fish stock so long as multi-species fishing remains significant. For example, no reasonable limit to the mid-water trawl fleet alone could produce appropriate harvest levels for Pacific Ocean perch. If fishing rates are uncontrolled by license limitation, conservation of fish stocks must still be sought through direct harvest limits, such as annual quotas. Imposing licensing on top of traditional harvest controls could only reduce the potential for fishing fleet over-capitalization. Finally, to be successful, this approach to economic efficiency in commercial fishing would require either strict limits on technological upgrading of fishing vessels and gear, or a license buy-back or vessel retirement plan to cancel the expanding harvest capacity.

In sum, license limitation has three principal drawbacks as an economic regulation for Pacific groundfish. First, it requires substantial supplementary regulation to assure fish stock conservation. Controlling aggregate multi-species fishing capacity does not prevent significant over-fishing of more economically profitable fish stocks. Second, additional controls, besides licenses, must be placed on fishing capacity. License limitation does not eliminate economic incentives for individual fishermen to increase investments in fishing capacity that are superfluous in the aggregate. Finally, licensing programs would tend to restrict license-holders to specific fish stocks or other sub-units of the fishery and may unreasonably restrict the use of more flexible, multi-purpose vessels. On a positive note, license limitation is one attempt to limit the cost of "inputs" to the fishery. There may be sub-units of the fishery (mid-water trawlers, or sablefish traps?) that could be economically regulated by license limitation.

Properly controlled and enforced, individual fisherman quotas could overcome many drawbacks of the license limitation approach. Since quotas would be issued for individual species, the quota system would automatically incorporate biological conservation as well as economic efficiency objectives. Assuming marketability of quota rights, vessel operators can choose to fish a mix of species or operate in the combination of fisheries that most suits them. A vessel owner with quantitative rights in widow rockfish, for example, could sell these rights and move into a nearshore fishery or to an Alaskan fishery. Similarly, fluctuations in the shrimp fishery may cause a flow of vessels between the shrimp and groundfish trawl fisheries. With quantitative rights, this flux can be accommodated by an exchange of individual quotas; no vessel need to eliminated completely from either fishery. In this respect, the individual quota system is much more flexible, while the license system essentially assigns a certain number of vessels to each fishery.

Individual quotas have two major benefits: fishing vessels have greater operational flexibility and there is increased potential for harvesting industry efficiency. Such quotas may, however, be expensive to enforce. Under-reporting and mis-reporting of species will directly affect the quota system's credibility. For this reason, enforcement will have to be on an individual vessel basis, catch sampling will have to be quite refined, and sample timing carefully guarded. If biological yields are defined on sub-areas of the fisheries, the individual quotas will have to follow suit. Whether enforcement becomes a major problem depends largely on whether the system creates conservation-minded fishermen who police themselves.

Enforcement is a problem, but the groundfish fishery would seem more likely candidate for quantitative rights than, say, the salmon fishery, simply because detection of serious transgressions would be easier. Unloading tons of fish from a trawl vessel is difficult to conceal. This, and the relatively small number of locations where unloading occurs, should make enforcement manageable.

The individual quota approach could be introduced on a partial basis. Without causing any serious dislocation in the trawl fleet, individual quotas could be assigned for Pacific Ocean perch, widow rockfish, Pacific whiting or any other species for which there is a firm optimum yield estimate. Reservations on the part of fishermen and managers could be tested in this way without converting the entire management system at once. License limitation, in contrast, tends to be a once-and-for-all, all-inclusive event. By testing the approach on a particular fish stock, preferably one that is fully used and subject to "target" fishing, both managers and fishermen could learn what specific adaptations to make in the system.

CONCLUSION

Groundfish management on the Pacific Coast has evolved a detailed set of administrative procedures and regulations, based substantially upon the preceding state and international regulations, and keyed to the biological conservation needs of the principal commercial fish stocks. The Pacific Fishery Management Council pioneered development of "framework" management plans, incorporating specific rules for modifying the optimum yield, acceptable biological catch levels and harvest regulations both within and between fishing seasons. In this, and in its breadth of coverage, the Pacific Coast groundfish FMP can be judged a substantial, state-of-the-art management document.

There is room for further improvement in two aspects: incorporating multi-species considerations and non-biological objectives in setting levels of optimum yield, and restructuring the fishing rights by limiting access to achieve a greater degree of economic efficiency. Since multi-species fishing, and multi-purpose fishing vessels are common in the Pacific coast fishery, it seems clear that more attention should focus on determining ecological implications of fishing for the stocks that are heavily exploited by the commercial fishery. For example, Pacific whiting may be a major predator of shrimp, juvenile fish or other stocks. This could have a major bearing on optimum yield for whiting fishery. Also, the problem of aggregating several optimum yields from jointly fished species (such as in the *Sebastes* complex) needs further consideration. Simple models of multi-species fisheries suggest that the optimum for the mixed stock should not, as suggested in the FMP, equal the sum of the maximum yields for the individual constituent stocks. These problems of biological optimum yield are on the leading edge of fishery management practice.

While the FMP contains various sections and references to non-biological criteria for optimum yield, close scrutiny of the management regime reveals very little explicit consideration of economic and social fishery objectives. In regard to the non-equilibrium optimum yield policies for Pacific Ocean perch and widow rockfish, this has left the managers with no rigorous foundation for fishing strategies chosen. Application of well-known economic principles to the choice of re-building and stock liquidation strategies could help to bolster the council choices. This would require more systematic information regarding the economic effects of deliberately altering the fish stock size over time--an aspect of management policy currently not well-expressed by the static, biological MSY and ABC guidelines.

Besides improving the substance and appearance of procedures under the existing management system, it would be useful to consider adopting limited access. Based upon a review of the two most likely alternatives, license limitation and individual fisherman quotas, it appears that both would have strengths and weaknesses in the Pacific coast groundfish context. License limitation has generic weaknesses, requiring supplementary restrictions on annual harvests and on technological upgrading of fishing capacity among licensed vessels. Besides improving the substance and appearance of procedures under the existing management system, it would be useful to consider limiting access. Based upon a review of the two most likely alternatives, license limitation and individual fisherman quotas, it appears that both would have strengths and weaknesses in the Pacific coast groundfish context. License limitation has the generic weakness that it leaves unaltered the individual fisherman's economic incentive to compete for shares of the harvest through costly expansion of fishing power. Consequently, annual harvest quotas for the fishery are still needed. Further, to achieve a reasonable degree of cost minimization with a licensing program requires supplementary restrictions on technological upgrading of fishing capacity. Individual fisherman quotas could avoid some of these difficulties. Given a known share of an annual allowable harvest, fisherman are encouraged to seek lower fishing costs in order to improve profits. Still, license limitation is now widely understood and relatively easy to enforce. As a first step in limiting access to the fishery, limiting licenses for groundfish would probably provide some useful control over further increases in fleet overcapitalization.

The logic of individual quotas seems strong, but there is no substantial experience to back it up. Consequently, the drawbacks and weaknesses may not be properly anticipated. Aside from the difficulty in achieving acceptance of a new approach, one problem might be enforcing individual quotas. Whether this and other problems would militate against individual fisherman quotas is not known. Fortunately, the approach could be introduced one step at a time, so that discovering and correcting errors could be part of the system.

In summary, groundfish management on the Pacific coast has come a long way in the past four years. A most ambitious and innovative management plan has been implemented, and the success of biological conservation objectives seems assured. Fine-tuning the optimum yield concepts to incorporate multi-species interactions is a logical next step for the research program. Serious consideration of alternative forms of limited access should begin immediately so that future decisions on this can proceed swiftly and with a reasonable chance of success.

LITERATURE CITED

Adams, P.B. and W.H. Lenarz. 1980 unpublished. Some estimates of the ability to target on species and species groups in the Northeastern Pacific otter trawl fishery. Tiburon, CA: NMFS Tiburon Laboratory.

Anderson, L.G., ed. 1981. Economic analysis for fishery management plans. Ann Arbor, MI; Ann Arbor Scientific Publishers, Inc.

Crutchfield, J.A. 1975. An economic view of optimum sustainable yield. In *Optimum sustainable yield as a concept in fisheries management*, P.H. Rodel, ed. Washington D.C.: American Fisheries Society Special Publication No. 9.

Fraser, G.A. 1979. Limited entry: experience of the British Columbia salmon fishery. *J. Fish. Res. Bd. Can.* 36:754-763.

Gunderson, D.R. 1983 in press. The great widow rockfish hunt of 1980-1982. *North Am. J. Fishery Management.*

Hobson, E. and W. Lenarz. 1977. Report of a colloquium on the multi-species fisheries problem, June 1976. *Marine Fish. Rev.* 39:8-13.

Huppert, D.D. 1979. Implications of multipurpose fleets and mixed stocks for control policies. *J. Fish. Res. Bd. Can.* 36(7):845-854.

Larkin, P.A. 1977. An epitaph for the concept of maximum sustainable yield. *Trans. Am. Fish. Soc.* 106:1-11.

Marasco, R.J. and J.M. Terry. 1982. Controlling incidental catch, an economic analysis of six management options. *Mar. Policy* April 131-139.

Mercer, M.C., ed. 1982. Multi-species approaches to fisheries management advice. Ottawa, Canada: Department of Fisheries and Oceans, Special Publication of Fisheries and Aquatic Sciences No. 59.

Meyer, P.A. 1983. A report concerning multi-species limited entry in selected coastal fisheries of Washington, Oregon and California. La Jolla, CA: Final report to the NMFS Southwest Fisheries Center.

Orbach, M. 1977. Report of the national workshop on the concept of optimum yield in fisheries management. Washington, D.C.: NOAA, U.S. Department of Commerce.

Pacific Fishery Management Council. 1982. Pacific Coast groundfish plan. Portland, OR: PFMC.

Pearse, P.H. and J.E. Wilen. 1979. Impact of Canada's Pacific salmon fleet control program. *J. Fish. Res. Bd. Can.* 36:764-769.

Pearse, P.H. 1982. Turning the tide, a new policy for Canada's

Pacific fisheries. Ottawa, Canada: Department of Fisheries and Oceans Communications Branch.

Rettig, R.B. and J.J.C. Ginter. 1978. Limited entry as a fishery management tool. Seattle, WA: University of Washington Press.

Roedel, P.H., ed. 1975. Optimum sustainable yield as a concept in fisheries management. Washington, D.C.: American Fisheries Society Special Publication No. 9.

Scott, A. 1984. Catch quotas and shares in the fisheries as property rights. In Essays in honor of James Crutchfield, R. Pealy and R. Stokes, eds. Seattle, WA: University of Washington Press.

Silvert, W. and L.M. Dickie. 1982. Multi-species interactions between fish and fishermen. In Multi-species approaches to fisheries management advice, M.C. Mercer, ed. Ottawa, Canada: Department of Fisheries and Oceans, Special Publications of Fisheries and Squatic Science No. 59.

Stokes, R.L. 1979. Limitation of fishing effort: an economic analysis of options. Mar. Policy October: 289-301.

Stokes, R.L. 1983. Limited entry in the Pacific halibut fishery: the individual quota option. Seattle, WA: Northwest Resources Analysis.

Sturgess, N.H. and T.F. Meany, eds. 1982. Policy and practice in fisheries management. Canberra: Australian Government Printing Service.

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INTRODUCTION

Economic considerations in the management of anadromous fish habitat fall into two major categories: economic efficiency and economic equity. Assessing economic efficiency in resource management focuses on the costs and benefits obtained from alternative patterns of use. "Efficiency" implies maximizing overall benefits, minus costs. Techniques of cost-benefit analysis developed over the past few decades allow us to estimate monetary values of a wide range of resource-based activities. Commercial fishing, mineral extraction, logging, and livestock grazing are commodities that have a clear economic value. Economists are also interested in estimating values for noncommodity activities, such as recreational fishing, camping and back-packing, and preservation of natural sites. Because of both data and conceptual limitations, cost-benefit analysis does not always accurately estimate net economic benefits. Nevertheless, cost-benefit analysis is the best means of assessing the overall economic efficiency of alternative resource-management policies.

Economic efficiency, broadly defined, is the essence of the Water Resources Council (WRC) (1982) Guidelines, which require agencies to develop as one alternative a plan that reasonably ". . . maximizes net national economic development benefits . . . ." The guidelines further state that the recommended plan ". . . is to be the alternative with the greatest net economic benefit, unless the Secretary of a department or head of an independent agency grants an exception to this rule" (Water Resources Council 1982). Economic efficiency is also the essence of the USDA National Forest System land- and resource-management planning regulation stating, "The primary goal in formulating alternatives, besides complying with NEPA procedures, is to provide an adequate basis for identifying the alternative that comes nearest to maximizing net public benefits . . ." (U.S. Department of Agriculture 1982).

Economic theory provides no clear guidance on the "equity" of management alternatives; however, some generally recognized principles help define the fairness of any distribution of benefits. For example, arbitrarily impoverishing particular groups or denying access to long-standing resource users without compensating them are actions normally considered inequitable. They are examples of what economists call redistributions of income or wealth. Economic methods can be used to anticipate and measure the probable effects of redistributions by identifying specific groups or individuals bearing significant portions of the costs or receiving significant portions of the benefits of management choices.

This paper explores the effects of forest and rangeland management on the economics of commercial and sport harvest of anadromous fish. The overall effect that forest and rangeland management has on the net benefits to producers and consumers of anadromous fish, as well as the cost incurred by resource managers and owners, is included.

ECONOMIC DIMENSIONS OF ANADROMOUS FISHERIES IN THE PACIFIC

Commercial salmon harvests by all nations bordering the north Pacific Ocean have recently averaged over 221 million fish per year (table 1). The United States catches slightly more salmon than do Japan and the Soviet Union. Canada takes less than one-third as many fish per year as do the other three. The five major commercial species of salmon are sockeye (or red), chum (or dog), pink (or humpback), coho (or silver), and chinook (or king). Three additional anadromous salmonids occur in western North America--steelhead and cutthroat trout, and Dolly Varden.

Salmon fisheries are classified according to geographical separation, political boundaries, fishing gear used, and motivation for fishing (recreation, subsistence, or commercial livelihood). Table 2 shows the breakdown of catches by some of the more significant divisions. Commercial purse-seine and gill-net fishing occur in protected waters such as Puget Sound, the Columbia River, and the inside waters of Southeast Alaska. Commercial trolling dominates the ocean fishery in California, Oregon, and Washington. Trolling is significant in southeastern Alaska as well. Historically, some species of salmon (especially chinook, coho, and sockeye) were caught primarily by traps, "fish wheels," and dip nets during spawning runs (Netboy 1980). These fishing techniques were more effective and less expensive than ocean fishing, but they are now generally prohibited.

Table 1--Average annual north Pacific commercial salmon catches, 1976-80

	Sockeye	Chum	Pink	Coho	Chinook	Total
	- - - - - - - - - -	- - - - -	Thousands of fish	- - - - -	- - - - -	- - - - -
U.S.S.R.	910	4,744	55,730	1,116	171	62,671
Japan	3,787	29,838	24,885	2,228	401	61,139
Canada	5,534	1,958	8,620	3,309	1,458	20,879
United States:	22,460	8,058	38,469	5,495	2,194	76,676
Alaska	21,097	7,340	37,106	2,478	676	68,697
Washington	1,363	712	1,337	1,883	633	5,928
Oregon	0	6	25	896	333	1,260
California	0	0	1	238	552	791
Total	32,691	44,598	127,704	12,148	4,225	221,365

Sources: Fredin (1980), Food and Agricultural Organization (1981).

Table 2--Annual average catches by United States user groups, 1975-79

State	Commercial salmon				Recreational		Subsistence
	Purse seine	Gill net	Troll	Other gear	Salmon	Steelhead	
	- - - - - - -	- - - - -	- - - - -	Thousands of fish	- - - - -	- - - - -	- - - - -
Alaska	33,487	23,067	1,332	625	329	3	878
Washington	2,388	1,738	1,258	889	1,314	108	--
Oregon	--	229	1,110	--	425	155	--
California	--	--	840	--	137	NA	23
Idaho	--	--	--	--	3	6	--
Total	35,875	25,034	4,540	1,514	2,208	272	901

-- = These fisheries do not exist in these States.

NA = not available.

Sources: U.S. Department of Commerce, National Marine Fisheries Service (1976, 1977, 1981); International North Pacific Fisheries Commission (1982).

Commercial salmon fisheries consist of many independent operations with no more than a few crew members (Petry 1979). Many trollers and gillnetters are operated by only one or two persons. Nevertheless, about 33,000 workers fish commercially at least part time in United States salmon fisheries, using 20,000 vessels (table 3). At least 727 party-boat or charter-boat operators derive a substantial portion of their business from salmon anglers. Most salmon vessels fish other marine species as well. In 1976, for example, 8,169 of the 12,558 vessels reported landing salmon in Washington, Oregon, or California also sold some groundfish, crab, or albacore.[1] Many are fully employed in commercial fishing for only a portion of the year, however. In comparison, the average monthly employment in logging in Oregon, Washington, and California was about 28,000 in 1978. Logging is also seasonal; the number of people employed in logging at some time during the year is substantially more than the average monthly figure. The average monthly employment in the timber industries of these three States, including logging, sawmills, veneer and plywood mills, and pulp and paper mills, was about 129,000 in 1978.

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[1] Huppert, D.D.; Thompson, C.; Edwards, B. Annual summary files from the 1974 thru 1976 coastwide summary data base: contents and summary statistics. Unpublished Admin. Rep. LJ-82-29. La Jolla, CA: U.S. Department of Commerce, National Marine Fisheries Service, Southwest Fisheries Center; 1982. 46 p.

Table 3--Estimated number of fishing units and employment in salmon fisheries

State	Commercial fishing fleet				Party/charter boats
	Vessels by gear type used				
	Troll	Gill net	Purse seine	Crew	
	Number				
Alaska	872	3,500	1,244	11,032	--
Washington	2,601	3,169	396	7,889	414
Oregon	3,259	718	--	5,852	253
California	4,158	--	--	8,316	60
Total	10,890	7,387	1,640	33,089	727

-- = These fisheries do not exist in these States.

Sources: Pacific Fishery Management Council ("Third Draft Framework Plan for Managing Ocean Salmon Fisneries Off Washington, Oregon, and California," Portland, OR, 1983. 133 p.; "Proposed Plan for Managing the 1983 Ocean Salmon Fisheries Off of Washington, Oregon, and California," Portland, OR, 1963); Alaska Commercial Fisheries Entry Commission (1982); U.S. Department of Commerce, National Marine Fisheries Service (1981).

In recent years, commercial salmon fishing has grossed around $300 million to $400 million (table 4). The finished products (mostly canned pack, cured, and fresh or frozen fillets and steaks) have a market value of around $1 billion wholesale (table 5). Of this $1 billion in wholesale value, about $20 million to $40 million is produced in Oregon, Washington, and California. In comparison, the estimated wholesale value of timber products produced in Oregon and Washington was about $8.5 billion in 1978.

Table 4--U.S. commercial landings of Pacific salmon by species and total ex-vessel values, 1950-82

Year(s)	Landings						Ex-vessel value
	Sockeye	Pink	Chum	Coho	Chinook	Total	
	Millions of pounds						$ Millions
1950-54	89.6	101.9	73.8	38.5	39.2	343.0	43.4
1955-59	68.1	93.9	51.6	24.4	32.9	270.9	41.7
1960-64	71.5	124.7	52.6	26.2	26.4	301.4	51.6
1965-69	90.3	111.0	41.7	34.9	27.3	305.2	63.3
1970-74	82.4	69.0	52.4	36.0	29.9	269.7	97.2
1975-79	103.0	140.5	48.0	33.6	32.3	357.4	240.4
1980	207.6	253.5	84.9	39.3	28.5	613.8	352.4
1981	226.2	257.1	98.9	35.2	31.1	648.5	436.2
1982	200.2	221.5	92.0	59.2	34.6	607.5	392.0

Sources: U.S. Department of Commerce, National Marine Fisheries Service (1973); U.S. Department of Commerce, National Marine Fisheries Service (1971-82).

The salmon fishery--along with tuna and shrimp fisheries--is one of the three most valuable marine commercial fisheries in the United States, based on gross market value. Much of the increase in salmon market values since the early 1950's was caused by increased prices. The average ex-vessel price rose from $0.126/lb in 1950 to 1954, to $0.669/lb in 1975 to 1980. In recent years, huge runs of Alaska sockeye and pink salmon have caused a moderate drop in ex-vessel prices.

Recreational fishing expanded during the past two decades to become a major user of the salmon resource in certain areas--particularly in Puget Sound, the southern part of the Washington coast and Columbia River mouth, and the northern Oregon coast. According to State records, annual sport salmon harvests nearly doubled from an average of 546,000 fish per year in 1950 to 1954, to 1,018,000 fish in 1976 to 1980. Although the sport harvest does not rival the commercial harvest, major portions of the coho and chinook salmon catches are taken by recreational hook-and-line, and almost all of the steelhead are taken by recreational anglers.

Table 5--Quantity and value of processed fishery products from the United States' north Pacific salmon fisheries

	1976	1977	1978	1979	1980	1981
Pacific coast:						
Fresh and frozen--[1]						
Quantity (thousand of pounds)	4,129	3,153	4,111	3,042	1,582	2,826
Value (thousands of dollars)	8,281	7,015	9,885	6,282	4,263	7,863
Canned--[2]						
Quantity (thousands of cases)	156	243	16	53	18	167
Value (thousands of dollars)	17,121	25,824	1,798	5,825	4,169	17,336
Cured--[3]						
Quantity (thousands of pounds)	5,055	4,504	5,602	3,677	3,465	4,046
Value (thousands of dollars)	14,523	16,825	21,817	14,298	12,737	16,119
Alaska:						
Frozen--[1]						
Quantity (thousands of pounds)	50,578	76,674	121,419	149,211	195,404	283,265
Value (thousands of dollars)	101,438	170,589	291,955	308,134	526,553	788,150
Canned--[2]						
Quantity (thousands of cases)	2,512	2,651	3,409	3,109	4,175	4,445
Value (thousands of dollars)	190,745	180,753	242,260	286,422	400,060	440,911
Cured--[3]						
Quantity (thousands of pounds)	3,783	NA	NA	NA	NA	NA
Value (thousands of dollars)[4]	11,880	NA	NA	NA	NA	NA
Total Value	343,988	401,006	567,715	620,961	947,782	1,270,379

NA = not available

[1] Includes steaks and fillets.
[2] Standardized to 48 1-lb cans.
[3] Includes smoked fish, caviar, bait eggs, and salted fish.
[4] Actual values not available. These values estimated using average price for frozen products on the Pacific coast.

Sources: U.S. Department of Commerce, National Marine Fisheries Service (1975-81); The Fishermen's News (1983).

The economic importance of recreational fishing is more difficult to measure than that of commercial fishing because of the lack of market prices. Special fishing surveys in Washington, California, and Oregon estimate total recreational expenditures to be around $186 million per year for salmon and steelhead fishing trips (table 6). This figure includes travel, on-site, and gear expenditures. Another measure of economic value is the net amount the recreationists would be willing to pay for fishing over and above costs.

This net economic value for salmon angling is estimated to be about $83 million in Washington, Oregon, and California (table 6). Equivalent values are not available for Alaska because the necessary studies have not been performed.

Table 6--Estimated economic measures for recreational salmon and steelhead fishing

	Expenditures	Net value
	- - - - Millions of dollars	- - - -
Washington	126.3	42.5
Oregon	53.2	31.5
California	6.3	9.0

Sources and procedures:

1. Washington and Oregon expenditures from Sorhus and others (1981).
2. California expenditures estimated from 1976-80 average annual ocean salmon angler-days (179,820) and average expenditure per day for San Francisco area partyboat salmon anglers ($38.88) from 1979 National Marine Fisheries Service survey reported by Center for Natural Areas ("Survey of Partyboat Passengers to Summarize and Analyze Recreational Demand for Partyboat Fishing in California," Southwest Fisheries Center Administrative Report No. LJ-80-14C, La Jolla, CA, 1980. 75 p.).
3. Net-value estimates for Washington and Oregon are from Brown and others (1980). California net value is estimated by multiplying number of trips by $50, about midway between the estimated day-values for Oregon and Washington ocean salmon-fishing trips.

Subsistence fishing is important for residents of Alaska and for Native Americans in certain areas of Washington, the Columbia River, and the Klamath River. Native Americans constitute a growing portion of those fishing commercially. In Washington and Columbia River fisheries, they are increasingly using their historical fishing rights, which were established in Federal Courts. These rights allocate harvestable portions of the fish stocks that return to the "usual and accustomed" fishing places as specified by treaty. During 1976 to 1981, harvests by Native Americans increased from about 1 million to 3 million fish per year in Washington and the Columbia River. Because total annual harvests (treaty and non-treaty commercial plus recreational) remained between seven and eight million fish, treaty fisheries have taken an increasing share of the harvest in the region.

The north Pacific salmon and steelhead fisheries are extremely widespread, diverse, and economically significant. These fisheries provide employment to thousands fishing commercially and also shoreside workers. Often the fishery is one of the few livelihoods available in isolated coastal communities. Large numbers of salmon contribute to the subsistence of many people. Among recreational anglers in Alaska and the Pacific Northwest, salmon and steelhead fishing are extremely popular. Anadromous fish are thus a resource worthy of substantial consideration in resource-management decisions.

CONCEPTS OF ECONOMIC VALUATION FOR FISHERIES

To understand and properly use estimates of economic value, several related concepts must be distinguished. An economic value given to a particular resource or industry can be divided into those values accruing to consumers, producers, taxpayers, and resource owners. The economic value may be positive to one group, but negative to another. For any given target group, the value may be calculated as an "all-or-nothing" value or as a "marginal" value. An all-or-nothing value is the value of having resources or commodities, rather than not having them; the marginal value is the value of a small change in the quantity of the resource or commodity. Estimates of value can apply to one or more potential uses for a resource; for example, commodity value pertains to the increase in value when basic materials or resources are made into consumable goods, and amenity values often come from natural environments and in situ resources.

In practice, the economic value of some commodity or activity is measured as the dollar amount that consumers or business firms are willing to pay for the commodity. This "willingness to pay" can be expressed as an all-or-nothing value, representing the total amount consumers would pay to avoid going without the existing amount of the commodity. The marginal value--an increase or decrease in willingness to pay associated with a small increment or decrement to existing quantities supplied--is often more useful to know. Most forest- and rangeland-management decisions are concerned with marginal effects on commodity markets.

COMMODITY VALUES

Values of commodities are related to the market-demand curve (fig. 1). If consumers allocate their expenditures among commodities to maximize their well-being, they will purchase more of virtually any product when the price is low, and less when the price is high. This theory explains why the demand curve depicted in figure 1 slopes downward to the right. For any given consumption rate, there is a maximum price consumers will pay for an additional unit. This price is a useful measure of the marginal value of the product to consumers. Multiplying the price times the quantity demanded yields the gross market value.

Gross market value of harvests is commonly available for whole fish at dockside, processed fish at wholesale, and retail fish in final goods markets. Similar values can be computed for stumpage or forage, wholesale primary wood products or beef, or for finished wood products or meat in consumer markets. Although gross market value can be a useful indicator of industry size, it is of limited use in assessing economic benefits from an industry because it represents neither the value of the total supply to consumers, nor the net economic value accruing to producers.

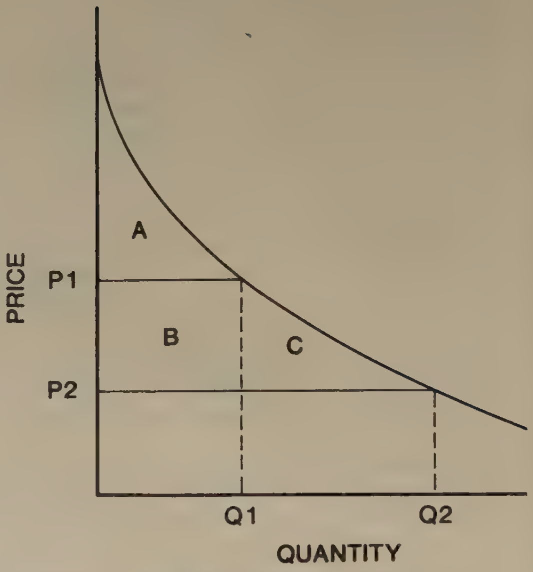


Figure 1.--Market-demand curve. If quantity increases from Q_1 to Q_2, market price would fall from P_1 to P_2. Total willingness to pay, for quantity Q_1, equals the area labeled A, plus the gross market value $P_1 \times Q_1$. Consumer surplus--the amount consumers are willing to pay above the amount they actually pay--for Q_1 is equal to area A.

When large changes occur in quantity supplied, the market price and underlying marginal value to consumers will change. If quantity supplied increases from Q1 to Q2 (fig. 1), the market price would fall from P1 to P2. Gross market value could rise or fall depending on whether the percentage change in price is less than or greater than the percentage change in quantity. Neither the change in gross market value, nor the change in quantity times the original price is a valid measure of the change in economic benefits. Consumers are better off with the lower price because they can still buy the original quantity and have money left over.

Economists use willingness to pay to measure the amount by which consumers are better off. For any given quantity consumed, the demand price represents the amount consumers are willing to pay for a marginal increase in consumption. If we value each unit--from the first one up to the actual quantity consumed--at its marginal value, the total willingness to pay would be measured by the area under the demand curve. For quantity Q1, for example, this total would equal the area labeled A plus the gross market value P1 x Q1. The consumer surplus--the additional amount consumers are willing to pay above the amount they actually pay--for quantity Q1 is equal to the area A. By similar reasoning, the increase in consumer surplus associated with an increase in quantity from Q1 to Q2, accompanied by a price decrease from P1 to P2, is represented by the sum of areas B and C. The change in consumer surplus is the most relevant measure of the change in benefits to consumers.

Producers, like consumers, may enjoy a surplus. The producer surplus is the excess of market value over the costs of production, where costs must include reasonable payments to labor, management, and capital, as well as payments for other raw materials. This surplus may be represented by profits earned by firms in the industry. The change in producer surplus is the most relevant measure of the change in benefits to producers.

Producers of natural-resource commodities usually draw on some resource stock such as a fish population, forest, or mineral deposit. When producers find that production of commodities from a particular resource is profitable, they should be willing to pay fees to the resource owner. In a private-enterprise economy with private-property rights established for natural resources, the fees actually paid contain two distinct components: an economic rent, and compensation for maintenance and other costs incurred by the resource owner. The rent is an economic surplus similar to a profit. Economic rent reflects the scarcity of a fixed, productive asset, whereas profit reflects the success of firms at generating revenues in excess of operating costs. When commodity producers also own the resource, or when publicly owned resources are provided free to producers, reporting of profits versus rents is muddied; the rental value of resources may be hidden in the reported profits of producing firms. Regardless of how the rental value of a scarce resource is reported in the industry's accounts, two distinct economic surpluses are to be included as benefits to the producer side of the market--profits and rents. Consequently, the total net economic value accruing to the economy through production of natural-resource commodities consists of consumer surplus, producer profits, and resource rents.

Market prices and monetary costs recorded by business firms provide information on economic values and costs. This is especially true if prices and costs are determined in a perfectly competitive market. A competitive market is one with sufficient numbers of buyers and sellers to prevent any one of them from establishing the going price, where all buyers and sellers are free to buy or sell as much as they want at the going price, and where property rights to the commodities being sold are well defined and exclusive. Exclusive means the rights to use, to exclude others from use, and to sell a unit of the commodity are vested in its owner. Under these conditions, market prices are a good measure of the marginal value to society, and the marginal costs of producers are a good measure of the marginal cost to society.

The same conclusions apply in other markets. If labor and capital markets are perfectly competitive, the wage rates and rates of return on capital observed represent valid measures of the full social costs of using these factors of production. Where competitive markets establish rents for natural resources, the rents represent the marginal value of the resource to commodity producers. In the United States, however, many resources are not sold competitively. Some markets are dominated by large firms that dictate prices, and--more importantly--for many resource commodities (especially those associated with the public good, such as air and water quality, natural fish runs, and environmental amenities), clear private-property rights have not been established. When property rights are insufficient to define the various rights and responsibilities of all resource users, free use of or competition for the resource often results in what economists call an externality. When logging operations damage salmon spawning gravels, an external cost is imposed on the salmon-fishing industry. Similarly, when salmon fishing is competitive for a common pool of fish, each person in effect imposes an external cost on others because fish are harder and more costly to catch when the available stock is smaller. Finally, competitive market allocation of land and of associated renewable and nonrenewable resources is uncommon on public lands administered by Government agencies. When competitive markets do not function or external costs are imposed by one firm on others, private market prices do not provide an adequate basis for measuring economic value.

The market for public forage does involve a payment by the rancher to the agency, but the price is determined administratively, not by a competitive market. The actual price paid may be higher or lower than the market price that would prevail if forage were allocated through competitive bidding. The market for publicly owned timber also involves a payment based on the amount harvested. In general, the payment is based upon an oral or sealed-bid auction. In those areas with sufficient competition for timber harvesting rights, the price is reasonably close to a competitive-market price. The conditions of sale are not necessarily typical of what would normally be found in an open and competitive market, however.

Because salmon fisheries are common property, administered through public agencies, no fees are paid to private owners. Traditionally, the responsible agencies charge no direct fees for capture of fish. States do charge annual license fees, and sometimes they collect a flat-rate poundage fee for fish landed. Thus, economic value of the anadromous fish resource cannot be calculated based on fees paid, but must be estimated, based on potential or actual net revenues. The potential rent from a fish stock can be roughly calculated as the ex-vessel value of harvested fish minus the minimum necessary harvesting costs. The quantity of harvest used in this calculation would be based on knowledge of the potential yield of the fish population, and the cost estimate would depend on knowledge of the best capture technology and associated costs. Expecting actual fisheries to generate a net economic value equal to this potential rent is unrealistic because of the common property status of the fish population and traditional fishery-management methods--which seek to conserve the fish stocks but do not encourage economically efficient harvesting. Actual net revenues from commercial fisheries are generally a small (if not vanishing) proportion of potential rent.

RECREATIONAL VALUES

Although recreational fishing values are expressed as value per fishing day or fishing trip--not value per fish--the demand curve still can be used for analysis. Using figure 1 as reference, suppose that price is replaced by cost of getting to a particular site and fishing there. Quantity is the number of times per season or year that the angler goes fishing. When costs per trip are lower, anglers go fishing more often; thus, the demand curve slopes down to the right. The main problem is that recreational fishing is not sold in private markets. Estimation of the recreational demand curve requires indirect information, such as expenditures, fishing participation patterns, and possibly other socioeconomic data on anglers. Furthermore, it requires application of complex sets of assumptions and models. For full explanations of the alternative procedures available, see Desvousges and others (1983), Dwyer and others (1977), Freeman (1979), or Huppert (1983).

Once a demand curve for recreational fishing is estimated, a consumer surplus value can be given to fishing. As in commercial fishery evaluation, a net economic value for a change in total quantity consists of the marginal value of the increment to consumers, minus the marginal cost of producing the increment. Recreational commodities differ from commercial ones, however, in that commercial goods are generally distributed widely, making market prices nearly uniform, except for differences in transportation costs. Recreation, however, cannot be shipped to consumers; consumers have to go to the fishing site and produce their own recreation. Consequently, the costs of recreational fishing will be higher for anglers more distant from fishing sites. The value of recreational fishing to an angler will be lower for more distant sites, because the costs to use them are higher.

Fishing values are often expressed as an average per fishing trip or fishing day. If used carefully, these unit-day values are good approximations of the value of recreational fishing. Table 7 is a summary of salmon- and steelhead-fishing value estimates compiled by Meyer (1982). The wide range of values is partly from variations in research methodologies and partly from variations in the quality of recreational fishing being studied. Some of the factors that make salmon and steelhead fishing a heterogeneous activity are accessibility, scenery, congestion, and catch rate at different fishing sites.

To evaluate fishery management properly, the marginal value of salmon added by management and enhancement should be known. Unfortunately, estimates of fishing-day values are not easily translated into estimated values of fish caught because the satisfaction of anglers depends on various attributes of the fishing trip. Relaxation, the challenge of dealing with natural hazards, the excitement of the hunt, communion with nature, and the provision of food are all valued by recreational anglers. The prevailing recreational catch rate represents just one quality variable. Greater catch per fishing day would mean higher quality fishing. Similarly, more tranquil and natural surroundings would represent an improvement in recreational quality to many anglers. Recent advances in assigning recreational values have made value estimates for increased catch rate more accurate.

Interactions between fishing and the fish population need to be examined in any comprehensive assessment of recreational fishing. Because salmon are available to recreational anglers as common property, any increase in catch rate caused by stock enhancement will attract additional fishing effort. This would shift the demand curve to the right in figure 1. More fishing, however, will cause some reduction in fish population, which will in the long run result in a lower catch rate than originally expected.

Table 7--Estimates of Pacific Northwest salmon and steelhead fishing values based on sport-fishing demand

Author	Recreational product	Year data collected	Estimated value per day	Value in 1980 dollars
			Dollars	
Brown, Singh, and Castle	Oregon salmon and steelhead	1962	13.70	39.02
Gordon	Idaho salmon	1968	8.00	19.81
	Idaho steelhead	1968	15.00	37.14
Brown, Charbonneau, and Hay	U.S. fishing (nonriver)	1975	22.00	35.20
	River salmon and steelhead	1975	51.00	81.60
Tuttle, Richards, and Wahle	Columbia River salmon and steelhead	1975	28.00	44.60
Brown, Sorhus, and Gibbs	Pacific Northwest salmon and steelhead	1977	45.00	63.94
Crutchfield and Schelle	Washington ocean salmon	1978	18.19	24.01

Source: Meyer (1982).

In specific circumstances, fishing-day values may be used in estimating the value of improved anadromous fish stocks. For example, recreational and commercial fishing seasons for coho salmon off the coasts of Oregon and Washington have been strictly limited in recent years to achieve desired spawning escapement. An increase in fish-run size would result in increased season length. If lengthened seasons would create additional fishing days with uniform quality, the increased value of recreation could be estimated by the product of average fishing-day value and the increment in number of days fished.

COMMERCIAL
seasons
enforcement
species
RECREATION
area
gear size
fish limits

MANAGEMENT OF ANADROMOUS FISHERIES

A proper evaluation of how forest and rangeland management affects anadromous fish stocks requires estimates of economic and other benefits originating from the fisheries, and estimated costs of the forest and range industries, and of the Government agencies responsible for the management. Economic performance of salmon fisheries, however, largely depends on the management procedures of the responsible agencies.

BIOLOGICAL CHARACTERISTICS AND OBJECTIVES

Each salmon population spawning in a specific river or stream is treated as a separate stock. Fish populations are sometimes further subdivided according to the spawning season (for example, Columbia River "fall" chinook salmon). The sustainable yield of each stock depends on such factors as extent and quality of spawning gravel, and extent and quality of rearing habitat (including streamflow, cover, dissolved nutrients, and food supply). Additional factors include mortality during upstream and downstream migrations, and ocean survival. Because fishery managers control the quantity and timing of harvests only during the ocean-feeding stage and during the spawning migration of the fish, population models developed for fishery management assume a given size and quality of freshwater habitat.

One such model, a "spawner-recruit" curve (fig. 2), pertains to a group of coho salmon stocks spawning in Oregon coastal streams (Oregon Department of Fish and Wildlife 1982); however, curves for other species and stocks are similar. On the horizontal axis is an estimate of adult coho salmon reaching spawning sites in Oregon streams. Spawning stock size is plotted versus number of adult fish recruited to the fishery 3 years later (the typical time between generations). The fitted curve predicts the run size resulting from any given spawning stock, and the diagonal line is the replacement line. If the recruitment of spawning stock falls above the 45-degree line, the progeny more than replaces the spawning stock. The excess of recruitment over spawning-stock size can be harvested without causing a reduction in original stock size.

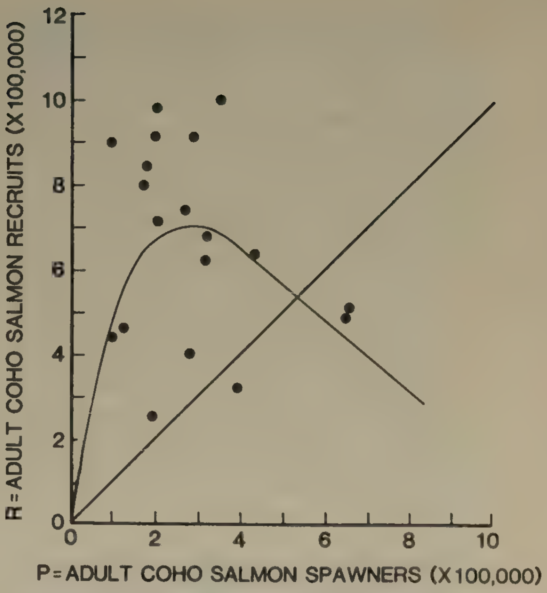


Figure 2.--Spawner-recruit curve for Oregon coastal coho salmon (adapted from Oregon Department of Fish and Wildlife 1982).

Maximum recruitment is achieved at some spawning-stock size intermediate between zero and the maximum observed (fig. 2). One biological basis for fishery management is maintenance of the spawning population to achieve maximum recruitment. Because spawning fish have survived the ocean-feeding migration and escaped the fishery to return to spawning sites, spawning-stock size and escapement are often used interchangeably. The great variability of the run sizes about their expected values is caused both by natural fluctuations in reproduction and survival of fish, and by errors in measuring the numbers of spawners and recruits. Because of the inherent variability, maintaining a maximum run size is impossible. Even if the escapement is successfully maintained to achieve the maximum run-size every year, the annual harvest would fluctuate widely.

Achievement of escapement objectives is complicated by the tendency of many salmon stocks to mix in the ocean. Variations in timing and location of oceanic migrations make it difficult to predict what proportions of each stock will be caught in a particular area. Consequently, some less-productive stocks tend to be overfished and some highly productive stocks may be underfished by a mixed-stock fishery. This problem is particularly evident when hatchery stocks mingle with natural-spawning stocks, and are then jointly harvested. Because hatchery stocks tend to have high upstream-migration survival and very high smolt production per spawner, they can sustain a higher exploitation than naturally spawning salmon stocks.

ECONOMIC CHARACTERISTICS AND MANAGEMENT OBJECTIVES

Because of the common-property status of anadromous fish populations, competitive fishing by commercial fleets in the face of high prices would rapidly deplete stocks and severely reduce long-run economic returns. To prevent this, management agencies have historically controlled annual harvests by increasing costs of harvest rather than by reducing fleet capacity. Consequently, very little net economic return from publicly managed salmon fisheries can be expected.

The revenue and cost curves in figure 3 rely on concepts from population biology and economics. When recruitment exceeds replacement, the fishery can take the surplus without reducing subsequent run size. This surplus is equivalent to a sustainable annual yield. To construct the sustained-revenue curve, we further assume that any catch corresponds to a given fishing effort, here represented as vessel-days and measured along the horizontal axis. The total-revenue curve represents this sustained yield times market price. Total cost is equal to fishing effort times cost per unit of effort. For simplicity, both the fish price and the cost per unit effort are assumed to be independent of harvest. See Anderson (1977) for less simplistic versions of the model.

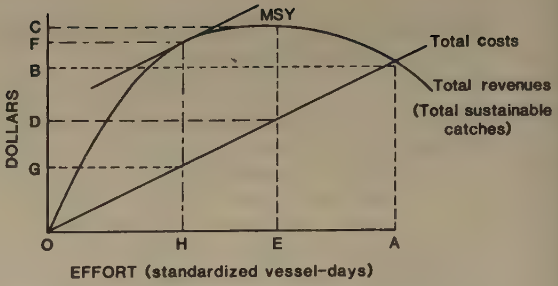


Figure 3.--Bioeconomic model of the fishery. Economic efficiency corresponds to the effort represented by point H. Economic equilibrium with open access occurs where revenues just cover all private costs of fishing, with effort at point A and revenue at point B. Because point A is to the right of the maximum sustainable yield (MSY), overharvest (in the biological sense) would be expected--but it would depend on how high the price is relative to the cost of effort.

With open access and no regulations, the competitive fishing fleet can be expected to grow until prospective profits of a new vessel are zero. Economic equilibrium occurs where revenues just cover all private costs of fishing. From a strict economic-efficiency perspective, such a resource has no value because the revenue produced is consumed in paying for the capital and labor used to harvest the fish. In fact, it would have a negative value because no surplus is left to pay for costs of managing the resource. In figure 3, this point occurs with effort at point A and revenue at point B. Because point A falls to the right of the maximum sustainable yield, this open-access fishery is expected to overharvest the stock in the usual biological sense. The extent to which this overfishing occurs in any particular case depends on how high the price is relative to the cost of effort. With a higher price or lower cost per effort, the fleet would be expected to stabilize with higher effort. With lower prices or higher costs, the fleet would stabilize with a lower effort.

Economic efficiency, which requires that the difference between revenues and costs be at a maximum, corresponds to the effort represented by point H. At this point, the slope of the revenue curve is equal to the slope of the total cost curve. At any effort greater than H, cost is increasing faster than revenue, which means that each additional unit of effort adds more to costs than to revenues. In other words, the marginal cost exceeds the marginal revenue. At any point below H, where marginal revenue is greater than marginal costs, increasing the amount of effort in the fishery makes sense. Thus, point H and the corresponding harvest are economically efficient; they give a maximum economic yield. This maximum economic yield represents the potential amount of economic rent that could be earned by a sole owner of the fish stock, if such an owner existed.

Traditional techniques of fisheries management, such as gear regulation, season closure, and quotas, all reduce catches to achieve escapement objectives; however, they tend to raise costs of fishing. To obtain a stable open-access fleet size with effort level E, cost of effort must increase until the cost curve intersects the yield curve at the MSY point. This solution is little better than the solution with open access; the total value of the resource is consumed in paying for the capital and labor used to harvest the fish, and no surplus remains to cover the cost of managing the resource. Once this point has been achieved, a price increase that raises the revenue curve further will have to be followed by more restrictions on the fishing fleet to raise costs again. Fishing costs increase through a variety of mechanisms. A reduced fishing season, for example, results in higher fixed costs per fishing day. Limiting the use of the most effective fishing gear reduces the catch per fishing day and raises costs per unit harvest. Rising salmon prices over the past two decades, coupled with traditional management tools for achieving escapement objectives, have led to repeated increases in fleet investments and decreases in fishing opportunities for each vessel operator.

To maintain low costs while controlling the fishing fleet's harvest, fishing effort must be managed in specific ways. In recent years, management methods--such as effort control, economic rationalization, and limited entry--have been discussed and evaluated by several national and international conferences (Fisheries Research Board of Canada 1979, Rettig and Ginter 1978, Sturgess and Meany 1982). Economically efficient management requires one of two approaches: creating financial disincentives to excessive fishing effort, or establishing a private property-like right to fish. The first approach could include landings taxes or royalties, and the second could include annual individual quotas. Both represent radical departures from previous management of North American fisheries, and are not being widely accepted. These ideas are not without precedent in public-resource management, however. Royalties are collected from most mineral extraction firms on public lands, and allocation of annual forest harvests (by auction or other methods) is analogous to the individual fisherman quota.

A first step toward economic rationalization in fisheries was license limitation. Limiting licenses prevents expansion of the fishing fleet during periods of rising fish prices, and thus works toward reducing overall harvest costs. License limitation was initiated in British Columbia in 1968; Alaska began its limited entry program in 1974; and Washington, Oregon, and California began a joint, cooperative license-limitation program for salmon in 1978. The details and restrictiveness of these programs differ widely among States, and the economic consequences depend on the progress made in reducing fleet sizes and in preventing compensating increases in fishing capacity per vessel.

Much of the effectiveness of license limitation is nullified, however, because such limitation does not prevent increased investment in fishing capacity within the existing fleet size. Most license-limitation programs eventually add some form of capacity limitation to each license. In British Columbia, replacement vessels are limited to the tonnage of the previously licensed vessel. California requires replacement vessels to be declared equivalent in fishing capacity by an expert review board. These provisions make license limitation more effective, but they may not prevent operators from increasing the capacity of existing vessels. Thus, even among fisheries economists, license limitation remains a controversial subject, and license limitation has resulted in little economic efficiency among fishing fleets on the Pacific coast.

OTHER FISHERY-MANAGEMENT OBJECTIVES AND CONSIDERATIONS

As with most public resources, a variety of special considerations and objectives guide fishery-management decisions. Most important objectives are stated in the Magnuson Fisheries Conservation and Management Act (MFCMA), the broadest piece of fisheries legislation to date. The MFCMA establishes Regional Fishery Management Councils to develop marine fishery-management plans for use by the U.S. Department of Commerce. The MFCMA sets out national standards for fishery management, which include: preventing overfishing, achieving "optimum" yields, promoting efficiency in the use of resources, and minimizing costs "where practicable." Optimum yield is defined broadly enough to include adjustments to escapement in anadromous fisheries for economic, social, or ecological reasons.

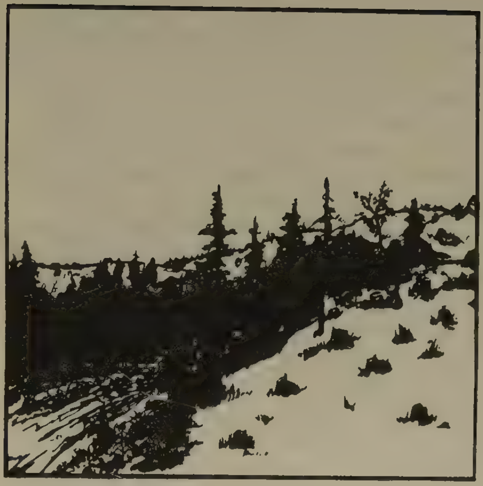
Current policies in fishery management attempt to maintain high fish populations and annual yields, while addressing socioeconomic factors such as maintenance of jobs and incomes in the many coastal communities that depend on the fishery. Another objective is the equitable division of available fish among competing user groups. The Pacific Fishery Management Council's Salmon Plan (1983), for example, provides for a 30-percent share of coho salmon for recreational fishing off the Oregon coast and the Columbia River. Also, allowable annual catches of salmon in the ocean-troll fishery are set with the intention of permitting the escapement of salmon to "inside" (protected water) net fisheries.

IMPLICATIONS FOR ECONOMIC EVALUATION OF ANADROMOUS FISH HABITAT

Given the economic problems of open-access fisheries under their existing management, how should we evaluate a prospective increase in salmon stocks contributing to the fisheries? In the commercial fishery, no net economic yield will occur when harvests are increased if more fishing vessels enter the fishery. Resource management authorities have consistently failed to generate a rental value for fisheries. This failure suggests that other objectives, such as fisheries employment or freedom of choice in fishing occupations, were considered more important. One could then argue that these other objectives must have been worth at least what was "paid" for them. Maintenance of additional employment in coastal communities, for example, could be counted as a benefit, but this argument assumes too much about the knowledge and intentions of public decisionmakers. If other social or cultural objectives are achieved at the expense of economic efficiency, they need to be evaluated and justified on their own merits.

Prospects for generating net economic yields from commercial fisheries are not so bleak as the simple bioeconomic model suggests, however, if recently established license-limitation programs prevent some of the potential new investment in the fishing industry. For marginal growth in anadromous stocks, one could assume that additional harvests involve no additional costs, because sufficient capacity is already available. Some increase in fishing effort would probably be necessary to take additional catch, however, and this effort involves some incremental cost. Thus, for increments taken by fishing fleets whose capacity is rigidly controlled, only the incremental costs of increased capital depreciation, consumable supplies, and labor hired away from alternative employment need be subtracted from market value to determine net economic value accruing to producers. Both Meyer (1982) and Crutchfield and others (1982) suggest that about 90 percent of gross ex-vessel value of marginal harvest is net value. This figure applies only so long as the fishing industry is prevented from expanding its capacity in response to the increased catch.

In addition to this net value in commercial fishing, consumer surplus is generated in both the commercial and recreational fishing sectors. Neither of these values has been sufficiently documented to be used for practical assessments, but both could be important in preserving and improving salmon habitat. Finally, nonmonetary factors, such as maintenance of fishing communities, cultural traditions, and a sometimes attractive lifestyle, must be counted as benefits of anadromous fish stock management. More comprehensive studies of these factors may allow us to assign a monetary equivalent to these benefits.



MANAGEMENT OF FRESHWATER HABITAT

DEPENDENCE OF ANADROMOUS FISH PRODUCTIVITY ON HABITAT

Anadromous salmonids of western North America have an extensive geographic range extending from the McKenzie River on Alaska's north slope to southern California. Habitats within this range are used by eight species of anadromous salmonids. Certain geographic areas are dominated by one species, but several species almost always cohabit within the range. Habitats within much of the range of anadromous salmonids are found in coniferous forests.

Anadromous salmonids use freshwater, estuarine, and marine environments to complete their life cycles. Habitat requirements are exacting for all species. All accessible freshwater environments, and an extensive variety of microhabitats, are used by anadromous salmonids at some stage in their life history. Most reproduction occurs in fresh water, although some species occasionally reproduce in brackish intertidal areas. Juveniles of most species rear in fresh water for some time before migrating to the sea where they mature. For optimum production all species require: water between 5.6 and 14.6 °C; free migratory access to and from the sea; clean gravel substrate, with less than 10 percent sediment smaller than 1-mm diameter, for reproduction; water with turbidity of less than 50 NTU (nephelometric turbidity units) during the growing season, for sight feeding; dissolved oxygen greater than 6 mg/liter in streams, lakes, and the intergravel environment; and invertebrate organisms for food (Everest and Harr 1982). Species preferences for these habitat variables differ slightly and are presented in detail by Reiser and Bjornn (1979).

Natural habitats are important in maintaining viable populations of wild anadromous salmonids. Because most waters support several species of anadromous salmonids, natural habitats must contain a diverse and complex set of depths, velocities, substrates, and cover, in addition to having adequate water quality, to meet the needs of several life stages of cohabiting species. Any environmental manipulations that simplify habitat will have a direct, negative effect on fish population structure and abundance. Because the ranges of anadromous salmonids and coniferous forests are largely coincident, forest management rather than range management will likely have the greater influence on salmonid habitat in the long run.

EFFECTS OF FOREST AND RANGELAND MANAGEMENT ON ANADROMOUS FISH RUNS

Links between forest management and fish production are complex and depend on many environmental variables. A physical disturbance created by forest management, interacting with the physical and biological features of the environment, can have either minor, major, or neutral effects on fish habitat. The general effects of forest management on habitat of anadromous salmonids have been documented by several studies. Effects range from drastic changes in physical habitat and fish populations to no apparent change in either habitat or fish numbers, depending on prescribed treatment.

Timber-management activities and logging-road construction have three primary effects on salmonid habitat. These activities tend to increase sediment and temperature in streams while reducing the source of large woody debris--the primary structural component of habitat in small streams. Other effects include changes in water chemistry resulting from timber cutting, burning, or use of forest chemicals, and an increased biochemical oxygen demand (BOD) caused by addition of fine organic debris to streams. Minor changes in streamflow also occur. A few studies have shown that these effects, singly or in combination, have decreased the standing crop of salmonids. Most studies, however, have only assessed the effects of timber management on habitat, rather than on salmonids, because assessing fish populations is a long-term, expensive operation. Consequently, the relation of habitat changes caused by logging to populations of juvenile salmonids needs further documentation (Everest and others, in press).

Salmonids are able to tolerate some short-term habitat disturbances because of their natural compensatory mechanisms, such as high reproductive rates and a fairly broad scope of physiological and behavioral responses. Salmonid populations have always had to cope with short-term natural habitat disturbances, such as floods, sedimentation from landslides, scouring of stream substrates, and deposition of organic debris in streams. These disturbances occur with varying frequencies and magnitudes, and may depress fish production in the short run.

The frequency of these events, however, is often accelerated by timber-management activities, and the construction and use of forest roads. Frequent occurrences sustained in intensively managed watersheds can produce cumulative effects that can cause long-term decreases in salmonid productivity.

These accelerated events, by themselves, probably would not completely eliminate salmonids from forested watersheds, even in a worst-case situation (Salo and Cederholm 1981). When the cumulative effects of logging activities on freshwater life-history stages are combined with an intensive harvest of fish stocks in both fresh and saltwater, however, and imposed over natural mortality rates of salmonids, fish production can drop below the level needed for desired seeding.

Removal of the forest canopy adjacent to and within the riparian area has the greatest effect on salmonid habitat. This removal raises summmer water temperatures (Moring and Lantz 1975), lowers winter water temperatures (Chapman 1962), and reduces the amount of terrestrial insect drop and litterfall into streams (Toews and Brownlee 1981). Canopy removal may also reduce bank stability, thereby increasing the amount of sediment entering the stream (Sedell and others 1982). In time, it will also reduce or eliminate the addition of large organic debris, which in turn will result in less structural complexity within the stream. Not all of the effects are detrimental, however; increased light reaching the stream can temporarily increase the production of algae and sustain greater densities of drifting invertebrates, which form the basic diet of fish.

Fauna and flora are often more abundant in sections of streams with open canopies than in forested sections (Aho 1976, Albrecht 1968, Erman and others 1977, Gregory 1980, Hughes 1966, LeCren 1969, Lyford and Gregory 1975, Murphy and Hall 1980, Newbold and others 1980, Thorup 1966). Removing streamside vegetation increases aquatic production at the lower end of the food chain. This production is a result of increased light, which stimulates growth of algae and periphyton (Gregory 1980, Murphy and Hall 1980). Many reports on logging effects, however, emphasize the destructive potential of accumulated sediment that adversely affects stream habitat (Cordone and Kelly 1961, Gibbons and Salo 1973, Iwamoto and others 1978). The long-term loss of large woody debris is equally detrimental. Thus, logging may have two opposing localized effects: canopy removal, tending to increase basic stream productivity; and sedimentation and loss of large woody debris, tending to decrease productivity.

Murphy and others (1981) found that small, open sections of streams passing through clearcuts had a greater density, biomass, or both of invertebrates and cutthroat trout than did shaded, forested reaches, regardless of sediment composition. They concluded that, for small streams in the Cascade Range, changes in fish-food status and increased production of algae resulting from shade removal masked or overrode effects of sedimentation. Their data indicate that strong links exist among amount of light reaching the stream, primary production, invertebrate production, and--ultimately--vertebrate production. Gregory (1980) found periphyton production in small streams in a western Oregon study area to be light limited. Chapman and Knudsen (1980) found that fish production in some Puget Sound streams was indirectly light limited.

Thus, canopy removal in small blocks can positively influence stream productivity, but cumulative effects of extensive cutting could cancel any potential benefits. Sedimentation and canopy removal both have adverse effects in the long run. Increases in sediment load can cause the stream to become wide, shallow, and unstable, often with a braided channel (Leopold and others 1964). Filling of pools with sedimentary material reduces suitable habitat for trout (Bjornn and others 1974) and damages spawning habitat. These effects of sediment are not usually observed in sites where large woody debris creates a stairstep channel profile, and forms plunge pools downstream of debris accumulations (Keller and Swanson 1979, Meehan and others 1977). Canopy removal and stream cleanup usually cause a substantial loss of the large woody debris that can mitigate the effects of sediment. Canopy removal rarely increases stream temperatures enough to kill trout (Martin and others 1981, Moring and Lantz 1975), but sublethal increases can indirectly affect survival, and cumulative effects can reduce the quantity and quality of rearing habitat in downstream waters.

Physical habitat for anadromous salmonids has been altered in the last two decades by a combination of increased sedimentation, channel sluice-outs, and excessive debris removal related to timber management. The cumulative result has been a loss of large, high-quality pools necessary for rearing juvenile salmonids and holding adult salmon before they spawn. Most high-quality pools in small streams are formed by large tree-sized debris.

Also, most high-quality cover in small streams is provided by large organic debris. Overzealous cleaning of the channel, or failure to provide a long-term supply of large organic debris after cutting, can turn a productive stream that is suitable for salmonids of a wide range of sizes and ages, into a marginal stream suitable primarily for underyearling fish (Bisson and Sedell, in press). Coho salmon and cutthroat trout habitat generally is reduced in this manner in exposed and cleaned streams. The loss of high-quality pools removes temperature refuges as well. Big pools, in both small streams and large rivers, tend to stratify thermally in summer, providing cool-water refuges in areas where cool surface water or ground water enters the stream and collects (Everest 1973).

ECONOMIC CHARACTERISTICS OF INSTITUTIONS

Like stocks of ocean and river fish, freshwater habitat also suffers from the common-property curse. Although a variety of legal and administrative institutions allocate and assign rights to riparian areas and access to surface water, rights to much anadromous fish freshwater habitat remain unassigned. As a consequence, when an activity such as logging or mining damages the habitat, the damage does not appear as a cost of production to the offending firm. Without public regulations in sensitive areas, logging or mining can cause excessive damage to the habitat. Imagine some economically efficient system in which property rights to freshwater habitat are owned by private citizens (this is close to the actual situation in parts of the United Kingdom). Then, the habitat owner would require compensation from a logging firm up to an amount equal to the value of fishing lost. The logging firm would have strong, economic incentives to avoid habitat damage and to log where fishing values are least affected.

Under current laws, however, logging practices are publicly regulated. These regulations, in effect, are a substitute for the discipline of the private market that does not exist for habitat or fishery resources. Because regulations are formed in a public forum, various criteria for management of habitat need to be considered and agreed on.

ECONOMIC CRITERIA FOR MANAGEMENT

Each watershed, along with its anadromous fish stocks, forests, and rangelands, can be treated as a complex resource with multiple uses. Resource management should seek to raise the total net value of all resource uses. But some uses, such as fishing and logging, impinge on each other's potential value. Similarly, camping and backpacking may be incompatible with some forestry practices. Some different classes of recreational use, such as wilderness camping and developed motorhome camping, cannot use a given area simultaneously without conflict. Optimal use of forest lands requires balance among competing uses.

The broadest conclusion from economics is that each use should be adjusted until the marginal net value of one is equal to the marginal net value of all other uses. Thus, any increase in timber cutting should have a net economic value at least equal to the net economic value of fishing, camping, or other uses that is lost because of additional cutting. If the fishing or camping opportunities lost because of timber operations on a particular plot are worth more than the timber products, then the timber should not be cut. Where the timber value is greater than the fishery or recreational value, the timber should be cut. To achieve a balance in any case we need to know the marginal net values generated in fisheries, and the costs of efforts by management agencies and commercial enterprises to preserve or improve anadromous fish runs.

MARGINAL NET VALUES GENERATED IN FISHERIES

Improvements in freshwater habitat increase sustainable fishery yields for the major fisheries. Thus, marginal economic value in habitat management is expressed as the increase in harvest as a result of improved habitat times the marginal value of additional fish. Further, the value of additional sustainable harvest depends on how that harvest is allocated among commercial, recreational, and subsistence fisheries.

If fishery managers had exact control over the allocation of fish among users, they could achieve maximum value by allocating to highest valued uses first. Noncommercial uses having a higher value than the commercial harvest would probably be satisfied first, and the remainder allocated to the commercial harvest. This allocation would have little effect on the commercial price of salmon because of their large international market.

Placing values on net changes in fishery production would be simplified under the above allocation because marginal changes in production would primarily be changes in commercial harvest. The commercial value would therefore be the relevant value for that marginal change in production.

Fishery managers, however, have neither the capability (as long as the commercial catch from mixed stocks in the ocean is large) nor the desire to allocate fish in that manner. Thus, the actual change in value from marginal changes in fish production is an average of values for different uses that is weighted by the proportional allocation.

The net economic values from commercial harvests may be quite low when open access allows excessive numbers of fishing firms to compete for limited quotas. All ocean salmon fisheries on the Pacific coast, however, are currently under license-limitation systems and have sufficient capacity to harvest additional fish. Thus, approximating the marginal net economic value of improved or restored fish runs as the ex-vessel price of fish, minus the marginal increase in operating costs required to take the additional catch, is becoming increasingly acceptable. Under these conditions, the net value of a small increase in fish may be 90 percent of the ex-vessel value. This figure ignores possible increases in consumer surplus in retail markets, but most improvements in freshwater habitat will be small enough to make this an acceptable simplification.

Marginal values of anadromous fish to recreational fisheries have not been reliably estimated. The daily value of recreational fishing is undoubtedly greater when the daily catch is increased, and the seasonal fishing value for any fish run is greater when the run is greater. But the contribution of an increased run to either a daily or seasonal catch depends on the nature of the fishery and the fish run. Thus, the incremental contributions of fish runs to recreational values are hard to estimate.

Subsistence and Indian-treaty fisheries have not been studied extensively by economists to estimate net economic values. From an economic perspective, fish harvested by these groups would be valued differently. The treaty fishery is primarily an assignment of property rights to harvest fish to a particular segment of the commercial sector. Special cultural considerations may attribute a high value to a portion of the harvest tied to cultural-religious traditions. Beyond that, the harvest going to commercial markets would be valued much the same as the remainder of the commercial harvest, and this value would apply to marginal changes in harvests. Because under Indian treaties fish are generally harvested by less costly methods than other commercial harvest, the net economic value per fish may be somewhat higher in the treaty fishery.

Subsistence fishing in Alaska is by law for personal use or barter only. Subsistence fishing was at one time open to all residents; now it is limited to people residing in rural areas and small towns. Because no qualifying income test is used, some subsistence fishing is done by people of above-average means. The net economic value of marginal changes in subsistence harvest is probably somewhere between the ex-vessel value of the commercial harvest and the replacement cost of the fish in the diets of subsistence users. As with treaty fishing, some portion of this fishery may have a cultural-religious aspect.

COSTS INCURRED TO PRESERVE OR ENHANCE ANADROMOUS FISH RUNS

Current State and Federal forest-practice guidelines in the Pacific Northwest require protection of fishery resources during all timber harvest operations. This protection can cause out-of-pocket or opportunity costs to responsible timber-management agencies, private timber companies, and contractors. Protection of fish habitat results in increased cost to timber managers in the following activities: constructing and maintaining roads; protecting riparian vegetation; and maintaining and protecting habitat structure within streams.

Roads affect fish habitat primarily by accelerating sedimentation, infringing on stream channels and floodplains, and restricting fish passage. To alleviate sediment and infringement problems, roads in steep, unstable terrain should be avoided, or located on or near ridgetops, using varied grades to take advantage of favorable topography. Adequate drainage relief should be provided (Wenger 1984), and fish-bearing streams should be crossed on bridges or open-bottom culverts. Construction standards often require minimum road width and full-bench subgrade. Roads built to lesser standards often accelerate erosion and stream sedimentation (Fredriksen 1970, Megahan and Kidd 1972) and degrade habitat. The exact benefits of these activities to fish production, however, are hard to determine and each case must be examined individually. Most features of road location and design that benefit fisheries also provide long-term benefits to forest transportation systems. Although roads built to new, demanding standards are more costly, they are also less subject to cut-and-fill failures, and require less maintenance and reconstruction than roads built to lower standards. A complete analysis requires that all of the benefits from such roads--to timber management, fisheries, and other resources--be included in the benefit-cost equation whenever road construction or reconstruction is planned. At the planning stage, estimating the increased cost of construction is relatively easy, but determining the benefits of reduced maintenance costs and of less closure time because of road failures is much more difficult.

Protection of riparian vegetation and instream fish habitat also requires out-of-pocket and opportunity costs for timber managers. Timber managers must often use specialized timber felling and yarding practices to maintain riparian buffer strips. Directional felling of timber away from buffer strips by lining or jacking is a proven way to protect riparian vegetation. Directional (uphill) felling on steep, broken terrain is also safer for felling crews and reduces breakage of old-growth timber (Burwell 1971, McGreer 1975), resulting in increased recovery of wood fiber. The costs of directional felling are about three times greater than for conventional felling, but the benefits of directional felling in old-growth timber stands, based on increased fiber recovery alone, are often sufficient to pay the added costs. Several private timber companies use this technique to increase their timber production.

Large woody debris in streams is a critically important structural feature of fish habitat in forested watersheds. Fallen trees with attached rootwads and limbs provide the diversity and complexity of habitats required by the different species of salmonids residing in streams of the Pacific Northwest and Alaska. Because wood in aquatic systems has a finite lifespan, forest managers must provide a streamside source of large trees that will enter the stream channel, in the form of large organic debris, more or less evenly over time. Leaving commercial timber in buffer strips for this purpose may represent a substantial opportunity cost. The placement of artificial stream structures to compensate for the removal of riparian trees can also be costly, however. For example, a sound Douglas-fir, 36 inches in diameter, has an estimated volume of around 3,000 board feet. The stumpage value of such a tree could range from under $300 to over $1,200, depending on market conditions and location of the tree. The cost of installing a gabion structure to maintain a desirable stream habitat may range from $500 to $1,500, depending on its dimensions.

Because physical and economic characteristics differ among locations, both commercial and recreational values of a given stream habitat will differ also. Economic reasoning suggests giving greater attention to habitat protection and improvement in some areas than in others. Less productive streams, for example, may justify more aggressive forest practices, and more productive streams should be more strictly protected. Similarly, where timber inventories are less valuable, more timber should be left standing to protect stream habitat. Taking such variable factors into account, however, requires a high degree of knowledge and confidence about both physical and economic systems. Uniform rules of forest and range usage are easier to put into effect.

PROBLEMS OF IMPLEMENTATION

Economic considerations set forth in this paper should, ideally, improve management policies for freshwater anadromous fish habitat; however, economic criteria cannot, and should not, dominate policy formulation. Translating economics into specific rules is often difficult and fraught with uncertainty because of both a lack of well-developed economic models and a lack of data. The economic value of commercial fisheries depends on biological-yield potential, harvesting costs, and market demands. But uncertainties in biological assessments of potential yields leave most practical management decisions with order-of-magnitude estimates. Furthermore, harvesting costs depend on management strategies in the fishery, as well as market prices of fuel and equipment used in fishing. Finally, fish prices are subject to a wide variety of influences other than those from the fishery or river system. These factors, and the lack of useful economic studies for most anadromous fisheries, dictate that economic considerations be taken only as general guidelines for management.

Management plans for freshwater habitat are particularly complex and numerous because anadromous fish move from freshwater streams through sensitive estuarine habitats to oceanic feeding grounds, and back to the stream of origin. Individual States and Nations often control only one portion of a fish population's full habitat, which makes unified management of a fish population difficult. The United States' Regional Fishery Management Councils, for example, manage the 200-nautical-mile Fishery Conservation Zone. But many of the chinook salmon from the Columbia River system migrate to the ocean off British Columbia and southeastern Alaska. Inter-regional and international negotiations are necessary for overall management of these fish runs. Landward of the 3-mile territorial limit, States have more authority than the Fishery Councils. Moreover, responsibility for freshwater habitat is split among various State agencies and Federal departments. The interweaving of responsibilities and authorities makes it difficult to turn economically efficient propositions into management rules.

The real choice of policies for freshwater-habitat management is severely limited. Federal and State agencies are often restricted by necessary international compromises. Legislatures rarely allow management agencies to start some of the more economically attractive management methods, such as landings royalties or creation of private-property rights to instream habitat. Given the limited alternatives for managing anadromous fisheries, the economic objectives that can be adopted are limited also. Nevertheless, management must strive to use available natural habitats efficiently by balancing marginal net economic values among alternative uses, and by fairly distributing the economic gains from resource use among participants and citizens.

METRIC CONVERSIONS

1 inch = 2.54 centimeters
1 mile = 1.609 kilometers
1 nautical mile = 1.852 kilometers
1 pound (lb) = 0.45 kilogram

LITERATURE CITED

Aho, R.S. A population study of cutthroat trout in an unshaded and shaded section of stream. Corvallis, OR: Oregon State University; 1976. 87 p. M.S. thesis.

Alaska Commercial Fisheries Entry Commission. Alaska's fishing fleets. Juneau, AK; 1982. 316 p.

Albrecht, M. Die Wirkung des Luchtes auf die quantitative Verteilung der Fauna in Fliessgewasser. Limnologica. 6: 71-82; 1968.

Anderson, L.G. The economics of fisheries management. Baltimore, MD: The Johns Hopkins University Press; 1977. 214 p.

Bisson, P.A.; Sedell, J.R. Salmonid populations in logged and unlogged stream sections of western Washington. In: Meehan, W.R.; Merrell, T.R.; Hanley, T.A., eds. Proceedings, symposium on fish and wildlife relationships in old-growth forests; 1982 April 12-15; Juneau, AK. [Publisher's location unknown]: American Institute of Fishery Research Biologists; [in press].

Bjornn, T.C.; Brusven, M.A.; Molnau, M. [and others]. Sediment in streams and its effect on aquatic life. Moscow, ID: University of Idaho; 1974; Tech. Completion Rep., Water Resour. Res. Inst. Proj. B-025-IDA. 27 p.

Brown, W.G.; Sorhus, C.; Gibbs, K.C. Estimated expenditures by sport anglers and net economic values of salmon and steelhead for specific fisheries in the Pacific Northwest. Corvallis, OR: Oregon State University; 1980; Pac. Northwest Reg. Comm. Contract No. 10790006. 88 p.

Burwell, D. Prevention of debris accumulation in streams by uphill felling. In: Krygier, J.T.; Hall, J.D., eds. Forest land uses and stream environment. Corvallis, OR: Oregon State University; 1971: 118-120.

Chapman, D.W. Effects of logging upon fish resources of the west coast. Journal of Forestry. 60(8): 533-537; 1962.

Chapman, D.W.; Knudsen, E. Channelization and livestock impacts on salmonid habitat and biomass in western Washington. Transactions of the American Fisheries Society. 109: 357-363; 1980.

Cordone, A.J.; Kelly, D.E. The influence of inorganic sediment on the aquatic life of streams. California Fish and Game. 47: 189-228; 1961.

Crutchfield, J.A.; Langdon, S.; Mathisen, O.A.; Poe, P.H. The biological, economic and social values of a sockeye salmon stream in Bristol Bay, Alaska: a case study of Tazimina River. Circ. 82-2. Seattle: University of Washington, College of Fisheries, Fisheries Research Institute; 1982. 39 p.

Desvousges, W.H.; Smith, V.K.; McGivney, M.P. A comparison of alternative approaches for estimating recreation and related benefits of water quality improvements. Washington, DC: U.S. Environmental Protection Agency, Economic Analysis Division; 1983. 333 p. Contract No. 68-01-5838.

Dwyer, J.F.; Kelly, J.R.; Bowes, M.D. Improved procedures for valuation of the contribution of recreation to national economic development. Urbana-Champaign, IL: University of Illinois, Water Resources Center; 1977; Res. Rep. 128. 218 p.

Erman, D.C.; Newbold, J.D.; Roby, K.B. Evaluation of streamside bufferstrips for protecting aquatic organisms. No. 165. Davis, CA: University of California, Water Resources Center; 1977. 39 p.

Everest, F.H. Ecology and management of summer steelhead in the Rogue River. Fish. Res. Rep. 7. Corvallis, OR: Oregon State Game Commission; 1973. 48 p.

Everest, F.H.; Armantrout, M.B.; Keller, S.M. [and others]. Salmonids. In: Brown, E.R., ed. Fish and wildlife habitats in managed forests of western Oregon and Washington. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region; [in press]: chapter 10.

Everest, F.H.; Harr, R.D. Silvicultural treatments. In: Meehan, W.R., tech. ed.. Influence of forest and rangeland management on anadromous fish habitat in western North America. Gen. Tech. Rep. PNW-134. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1982. 19 p.

Fisheries Research Board of Canada. Symposium on policies for economic rationalization of commercial fisheries. Journal of Fisheries Research Board of Canada. 36(7): 711-867; 1979.

The Fishermen's News [Seattle]. Pacific fisheries review. 1983 February: Vol. 39, No. 5.

Food and Agricultural Organization. Yearbook of fishery statistics. Rome, Italy: Food and Agricultural Organization, Fisheries Department; 1981. 151 p.

Fredin, R.A. Trends in North Pacific salmon fisheries. In: McNeil, W.J.; Himsworth, D.C., eds. Salmonid ecosystems of the North Pacific. Corvallis, OR: Oregon State University, Sea Grant Program; 1980. 331 p.

Fredriksen, R.L. Erosion and sedimentation following road construction and timber harvest on unstable soils in three small western Oregon watersheds. Res. Note PNW-104. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1970. 15 p.

Freeman, A.M. The benefits of environmental improvement. Baltimore, MD: Johns Hopkins University Press; 1979. 272 p.

Gibbons, D.R.; Salo, E.O. An annotated bibliography of the effects of logging on fish of the western United States and Canada. Gen. Tech. Rep. PNW-10. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1973. 145 p.

Gregory, S.V. Effects of light, nutrients, and grazing on periphyton communities in streams. Corvallis, OR: Oregon State University; 1980. 151 p.

Hughes, D.A. Mountain streams of the Barberton area, eastern Transvaal: Part 2. The effect of vegetational shading and direct illumination on the distribution of stream fauna. Hydrobiologia. 27: 401-438; 1966.

Huppert, D.D. NMFS guidelines on economic valuation of marine recreational fishing. NOAA Tech. Memo. NMFS-SWFC-32. La Jolla, CA: U.S. Department of Commerce, National Marine Fisheries Service, Southwest Fisheries Center; 1983. 43 p.

International North Pacific Fisheries Commission. Statistical yearbook, 1979. Vancouver, BC; 1982. 113 p.

Iwamoto, R.N.; Salo, E.O.; Madej, M.A.; McComas, R.L. Sediment and water quality: a review of the literature including a suggested approach for water quality criteria. EPA 910/9-78-048. Seattle: University of Washington, Fisheries Research Institute; 1978. 151 p.

Keller, E.A.; Swanson, F. J. Effects of large organic material on channel form and fluvial processes. Earth Surfaces Processes. 4: 361-380; 1979.

LeCren, E.D. Estimates of fish populations and production in small streams in England. In: Northcote, T.G., ed. Proceedings, symposium on salmon and trout in streams: H.R. MacMillan lectures in fisheries; 1968 February 22-24; Vancouver, BC. Vancouver, BC: University of British Columbia; 1969: 269-280.

Leopold, L.B.; Wolman, M.G.; Miller, J.P. Fluvial processes in geomorphology. San Francisco: W.H. Freeman and Co.; 1964. 522 p.

Lyford, J.H.; Gregory, S.V. The dynamics and structure of periphyton communities in three Cascade Mountain streams. Internationale Vereinigung für theoretische und angewandte Limnologie. 19: 1610-1616; 1975.

Martin, D.J.; Salo, E.O.; White, O.T. [and others]. The impact of managed streamside timber removal on cutthroat trout and the stream ecosystem. Seattle: University of Washington, College of Fisheries; 1981; Final Rep. FRI-UW-8107. 65 p.

McGreer, D.J. Stream protection and three timber falling techniques--a comparison of costs and benefits. Corvallis, OR: Oregon State University; 1975. 92 p. M.S. thesis.

Meehan, W.R.; Swanson, F.J.; Sedell, J.R. Influences of riparian vegetation on aquatic ecosystems with particular reference to salmonid fishes and their food supply. In: Importance, preservation and management of riparian habitat: Proceedings of the symposium; 1977 July 9; Tucson, AZ. Albuquerque, NM: U.S. Department of Agriculture, Forest Service; 1977: 137-145.

Megahan, W.F.; Kidd, W.J. Effects of logging and logging roads on erosion and sediment deposition from steep terrain. Journal of Forestry. 70(3): 136-141; 1972.

Meyer, P.A. Net economic values for salmon and steelhead from the Columbia River system. NOAA Tech. Memo. NMFS F/NWR-3. Portland, OR: U.S. Department of Commerce, National Marine Fisheries Service; 1982. 26 p.

Moring, J.R.; Lantz, R.L. The Alsea watershed study: effects of logging on aquatic resources of three headwater streams of the Alsea River, Oregon: Part 2: Changes in environmental conditions. Fish. Res. Rep. 9. Corvallis, OR: Oregon Department of Fish and Wildlife; 1975. 39 p.

Murphy, M.L.; Hall, J.D. Effects of clearcutting on predators and their habitat in small streams of the Cascade Mountains, OR. Canadian Journal of Fisheries and Aquatic Science. 38(2): 137-145; 1980.

Murphy, M.L.; Hawkins, C.P.; Anderson, N.H. Effects of accumulated sediment on stream communities in different trophic environments. Transactions of the American Fisheries Society. 110: 469-478; 1981.

Netboy, A. The Columbia River salmon and steelhead trout, their fight for survival. Seattle: University of Washington Press; 1980. 180 p.

Newbold, J.D.; Erman, D.C.; Roby, K.B. Effects of logging on macroinvertebrates in streams with and without bufferstrips. Canadian Journal of Fisheries and Aquatic Science. 37(7): 1076-1085; 1980.

Oregon Department of Fish and Wildlife. Comprehensive plan for production and management of Oregon's anadromous salmon and trout: Part 2. Coho salmon plan. Portland, OR: Anadromous Fish Section; 1982. 202 p.

Pacific Fishery Management Council. Third draft framework plan for managing ocean salmon fisheries off Washington, Oregon, and California. Portland, OR: Pacific Fishery Management Council; 1983. 133 p.

Petry, G.H. Pacific Northwest salmon and steelhead fishery report--the economic status of the Oregon and Washington non-Indian salmon gillnet and troll fishery. Pullman, WA: Washington State University; 1979. 177 p. Vol. 1.

Reiser, D.W.; Bjornn, T.C. Habitat requirements of anadromous salmonids. Gen. Tech. Rep. PNW-134. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1979. 54 p. (Meehan, William R., tech. ed.; Influence of forest and rangeland management on anadromous fish habitat in western North America; pt. 1).

Rettig, R.B.; Ginter, J.J.C., eds. Limited entry as a fishery management tool. Seattle: University of Washington Press; 1978. 463 p.

Salo, E.O.; Cederholm, C.J. Cumulative effects of forest management on watersheds - some aquatic considerations. In: Proceedings, Edgebrook conference on cumulative effects; 1980 June 2-3; Berkeley, CA. Berkeley, CA: University of California, Berkeley Press; 1981. 109 p.

Sedell, James R.; Everest, Fred H.; Swanson, Frederick J. Fish habitat and streamside management: past and present. In: Black, Hugh C., comp., ed. Proceedings, technical session on effects of forest practices on fish and wildlife production: Society of American Foresters annual meeting; 1981 September 27-30; Orlando, FL. Washington, DC: Society of American Foresters; 1982: 41-52.

Sorhus, C.N.; Brown, W.G.; Gibbs, K.C. Estimated expenditures by salmon and steelhead sport anglers for specified fisheries in the Pacific Northwest. Spec. Rep. 631. Corvallis, OR: Oregon State University, Agricultural Experiment Station; 1981. 86 p.

Sturgess, N.H.; Meany, T.F. Policy and practice in fisheries management. Canberra, Australia: Australian Government Publishing Service; 1982. 384 p.

Thorup, J. Substrate type and its value as a basis for the bottom fauna communities in running waters. In: Spec. Publ. 4. Pittsburgh, PA: University of Pittsburgh, Pymatuning Laboratory of Field Biology; 1966: 59-74.

Toews, D.A.A.; Brownlee, M.J. A handbook for fish habitat protection on forest lands in British Columbia. Vancouver, BC: Department of Fisheries and Oceans; 1981. 173 p.

U.S. Department of Agriculture, Forest Service. National Forest System land and resource management planning. Federal Register. 47(190): 43045; 1982. 36 CFR Part 219.

U.S. Department of Commerce, National Marine Fisheries Service. Salmon, 1947-72. Current Fish. Stat. No. 6129. Washington, DC; 1973.

U.S. Department of Commerce, National Marine Fisheries Service. Processed fishery products, annual summary. Current Fish. Stat. Nos. 7803, 8003, 8013, 8203. Washington, DC; 1975-1981.

U.S. Department of Commerce, National Marine Fisheries Service. Fisheries statistics of the United States, 1975. Stat. Dig. 69. Washington, DC; 1976.

U.S. Department of Commerce, National Marine Fisheries Service. Fisheries statistics of the United States, 1976. Stat. Dig. 70. Washington, DC; 1977.

U.S. Department of Commerce, National Marine Fisheries Service. Fisheries statistics of the United States, 1977. Stat. Dig. 71. Washington, DC; 1981.

U.S. Department of Commerce, National Marine Fisheries Service. Fisheries of the United States. Current Fish. Stat. Nos. 5900, 6100, 6400, 6700, 6900, 7200, 7500, 7800, 8000, 8100, 8200, 8300. Washington, DC; 1971-1982.

Water Resources Council. Economic and environmental principles and guidelines for water and related land resources implementation studies; request for comment. Federal Register. 47(55): 12297; 1982.

Wenger, K.F., ed. Forestry handbook. 2d ed. New York: John Wiley and Sons; 1984. 1335 p.

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